CHARACTERISATION OF THE BIODIVERSITY AND BIOLOGICAL AFFINITIES IN THE FIRST FARMERS AND LAST HUNTER-GATHERERS FROM NORTHEAST IBERIA BY DENTAL MORPHOLOGY ANALYSIS

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Dissertation presented by **Diego López-Onaindia** in fulfilment of the requirements for the Doctorate in Biodiversity of Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia, Univesritat Autònoma de Barcelona, directed by:

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In Bellaterra at 16 June 2017

Dr. Maria Eulàlia Subirà **Diego López-Onaindia**

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Eskerrikasko Amaia, zubarik hau ez zan posible ixengo, zuk hartu dozu karga hau nirekin batera, berez karga hau eta ni bebai. Ez da gainera ordu luzien, nekien ta humore txarren karga bakarrik, zeu ixen zara zalantzak neukozenien nirekin aztertu dauzenak eta holan urten da aurrera lan hau.

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Belarriak

Hitzegiten dugunaren gutienez doblea entzuten
jakin beharko genukeela uste zuten,
sortaldeko jakintsuek, mihingain bakarra
eta belarri bi ditugulako

Halabaina, arrazoi berberagatik sentitzen dira
behartuta sortaldeko larjakitunak
entzuten dutenaren doblea hitzegitera

Joseba Sarrionandia Uriblearrea, Hitzen Ondoeza

ABSTRACT

The main subject of this dissertation is the biological aspect of the human transition from Mesolithic (9,500 cal BCE – 5,500 cal BCE) to Neolithic (5,600 cal BCE – 2,200 cal BCE) in the Northeast of the Iberian Peninsula, and the biological relationships among the Neolithic populations of the same area. How this process, called Neolithisation, occurred in Western Europe, and concretely in the Iberian Peninsula, has produced a major debate within archaeologists and anthropologists during many decades. The methodology used to address this question has been the study of non-metric dental traits.

The analysed sample comprises Mesolithic sites from along the Iberian Peninsula; Neolithic and Chalcolithic samples from the North and Northeast of the Peninsula, and Southern France; and Bronze Age samples from the North and Northeast of the Iberian Peninsula. In total, 100 sites have been analysed, where a minimum number of 1,391 individuals were recovered and 17,262 teeth analysed for this work.

The results indicate that prehistoric populations from the Iberian Peninsula since the Mesolithic presented a dental morphological pattern that is compatible, for most traits, to the Eurodont dental pattern described for current Western European populations. Additionally, although it has been recorded that environmental factors might affect tooth formation and morphology in individual levels, this did not happen in a population scale. Thus, dental morphology proved to be stable enough to provide reliable information on the relationships between human populations in this concrete case.

Moreover, it is observable that the Pre-Neolithic samples from the Upper-Palaeolithic and Mesolithic periods from the different areas of the Peninsula (Portuguese Atlantic coast, Cantabrian Fringe, and Eastern Mediterranean coast) were not biologically different between each other. In contrast, all of them were different from Italian samples from the same period.

Regarding the Early- and Middle-Neolithic samples, the results show that there were significant differences between some of them. For example, the sample related to the *Sepulcres de Fossa* culture in the coastal and pre-coastal valleys from Catalonia, significantly diverged from the same period's sample from the Solsonian region and Andorra (in the Catalan Pyrenees). These two groups diverged both in the geographical dispersion and the funerary practices. Moreover, both of them presented similar affinity values in relation to Early- and Middle-Neolithic samples from

Navarre, in the Upper Ebro Valley. In addition, when the samples were compared to Farmer groups from Southern France, the results showed that while those samples from the Provence and Rhône Valley did not present differences with any of the Iberian samples, those from inland areas near the Pyreneans differed from the Navarrean and Sepulcres de Fossa groups.

On the other hand, during the Chalcolithic and Bronze Age the differences between samples from the different areas of the Peninsula decreased, and in the Bronze Age there were no observable biological differences between the groups.

Finally, in regards to the relationship between Hunter-Gatherer and Farmer populations in the Iberian Peninsula, the current results show that this was heterogeneous. The Neolithic samples that biologically were closer to the Hunter-Gatherers were those from the Upper Ebro valley, while the samples from the Pyrenean and Mediterranean areas diverge in different directions from them. During the Chalcolithic the samples resembled more to the Hunter-Gatherers than in previous periods, and the Bronze Age population showed strong affinities to the Upper-Palaeolithic and Mesolithic sample. Hence, the process of Neolithisation was heterogeneous, with different impacts of incoming populations in the various areas of the Peninsula. Furthermore, the results indicate that the influx migh have two different origins, the Mediterranean coast and through the Pyreneans.

LIST OF MOST IMPORTANT ABBREVIATIONS

aDNA: ancient DNA
Amelx: amelogenin
ASUDAS: Arizona State University Dental Anthropology System*Axin:* Axin
BCE: Before Common Era
BL: Bucco Lingual
BMP: Bone Morphogenetic Proteins
BP: Before Present
CAG: Calcolitic
CAS: Cascajos
CPF: Cova de Panta Foix
D*lx*: Drosophila distal-less gene
Dspp: Dentin sialophosphoprotein
EBA: Early Bronce Age
Eda: Ectodysplasin A
EK: Enamel knots
Enam: Enamelin
FA: Fluctuating asymmetry FDI: World Dental Federation notation
Fgf: Fibroblast growth factor
HERS: Hertwig's Epithelial Root Sheats
HLA: Human Leukocyte Antigen
LBA: Late Bonce Age
LBK: Linear Pottery culture
Lhx: LIM homeobox gene familly
MBA: Mediun Bronce Age
MD: Mesio Distal
mDNA: messenger DNA
MDS: multi-dimenisonal scaling
MMD: Mean Measure of Divergence
MNI: Minimum number of individuals
Msx: Msh Homeobox gene
mtDNA: mitochondrial DNA
NEO: Neolithic
OMIM: On-line Mendelian Inheritance in Man
Pax: Paired box genes
PC: Principal Component
PCA: Principal Component Analysis
PEK: Primary Enamel Knot
Ptn: Pleiotrophin
Runx: Runt-related transcription factor
SD: Standard Deviation
SEM: Scanning Electron Microscope
SNP: single-nucleotide polymorphism
STR: Short tandem repeat
TMRCA: Time to the Most Recent Common Ances

TABLE OF CONTENTS

1. INTRODUCTION

The process of Neolithisation in Europe and concretely in the Iberian Peninsula has produced a major debate within archaeologists and anthropologists for many decades. The main question of these debates is whether this process occurred homogeneously on the continent or are there regional differences, and if this happened due to a demic diffusion or a cultural diffusion, or even by cultural evolution of Mesolithic societies. The analyses to answer these questions have been launched from many areas of archaeology and bioarchaeology (including anthropology). These studies have shown that Neolithisation in Europe varies in different regions. While the studies in order to determine the biological origin of the farming societies in Central and Eastern Europe show overall homogeneous results, this is not the case in the Iberian Peninsula, where the results are heterogeneous and the analysed sample sizes small. Therefore, the methodology applied in this work in order to address this subject is the study of the dental morphology of human remains for this period and area. This method has been selected due to different aspects. On one hand, the fact that due to the hardness of enamel, teeth are usually the best-preserved skeletal materials in archaeological contexts. And on the other, the ability of the dental non-metric traits to inform about ethnicity, migrations and different demographic events in human populations makes this methodology adecuate to address this question.

1.1. CHRONOLOGICAL CONTEXT: CLIMATE AND ARCHAEOLOGICAL RECORD

The establishment of warmer climatic conditions pending the end of the Last Glaciation, allowed the progressive dispersal of hunter-gatherer groups from the refuges to all the Iberian Peninsula, and the rest of Europe (Bañuls-Cardona *et al.*, 2014; Soomer & Nadachowski, 2006). This cooling tendency was only interrupted by the cold period of the Young Dryas (or Dryas III) around 11,000 BP, after which the Holocene started. The effect of the Dryas III in the Iberian Peninsula was only limited, and we know the last Palaeolithic hunter-gatherers that adapted to this climatic change by the late Solutrean and Magdalenian cultures (Barandiaran, 1998).

With the beginning of the Holocene the climate became warmer and wetter, which allowed the expansion of warm forest in many zones of the Peninsula. In parallel, the increasingly mild climate would influence the hunter-gatherer's lifestyles, and with time they would become less mobile because they would have more resources in the same area. Nevertheless, this was not a homogeneous process and three main phases can be differentiated in the Iberian area (Martinez-Pillado, 2010; Straus, 2008):

1. Preboreal period. It was the first period from the Holocene, dating between 10,200 and 8,700 BP. It is characterised for being warmer than the previous Dryas III period, but it is still cool and humid.
2. Boreal period. It corresponds to the period with a decrease in humidity that took place between 8,700 and 7,500 BP.
3. Atlantic period (Postglacial optimum). This was the period between 7,500 and 5,000 BP, when there was an increase in both temperatures and humidity.

The warming of the environment also affected the sea level as the glaciers melted. As suggested by Gutierrez-Zugasti (2009) on the Cantabrian coast, this rising of the water level was up to 35 metres, which reduced the coastline by 4 kilometres at some points until the Boreal period, which would eventually arrive to the present situation (45 m above and a coastline one km narrower). Thus, this elevation also incorporated seawater in the river streams creating rich environments called estuaries, where semi-sedentary human populations would flourish (Straus, 2008). The final consequence of this increasingly favourable environment was the development of agriculture and farming that benefited from a climate that allowed controlled food production from domesticated species. According to the recovered data, during the begining of the Neolithic Age, the valleys from the Northeast of the Iberian Peninsula would be formed by decidious tree especies, predominantly oak, typical of riverbank areas. At the same time, in the Pyrenaic contexts conifers were most common (Buxó & Piqué, 2008; Piqué, 2005; Ros, 1996).

Consequently, the Neolithic age is referred to as the New Age, when thecnological development of productive societies happened. This development came along with the domestication of animals and plants, and the gradual decrease of dependence on wild resources. During the Upper-Palaeolithic and Mesolithic, human groups depended on game and wild fruits and plants for subsistence. Hence, related to the availability of natural resources, Mesolithic groups had to be nomadic or semi-nomadic. In contrast, the ability to produce the necessary resources, and also the ability to manage its disposal through the year, allowed Neolithic groups to become sedentary.

Related to these characteristics, the size of the groups would also evolve as they became sedentary, increasing their sizes. In fact, Mesolithic mobile populations would consist of small groups, which mainly lived in rock shelters or caves that would be temporary, while advanced Neolithic groups would live in open-air built villages that allowed them to grow in number of individuals (Barandiaran, 1998).

The available archaeobotanical data show that after 7,000 BP (c. 5,050 BCE) aridity increased in the Northeast of the Iberian Peninsula, which might be linked to a disminution of precipitations and human activity (Riera & Esteban, 1997). Moreover, from the IV millenium BCE onward, esclerophilic taxons increased their presence as oak forests were substituted by holm oak and cork oaks. This change has been related to the previously observed increasingly dry climate, but also to the intense human activities that led to deforestation in order to obtain cutivable open spaces (Piqué, 2005; Riera & Esteban, 1997; Riera et al., 2007; Ros, 1996).

Therefore, the presence of Neolithic in the archaeological record is related to the discovery of pottery, polished instruments, a differentiated lithic and bone industry, and domesticated faunal or agricultural remains (Alday, 2009). This definition on when we can consider a sample Neolithic or not is necessary to establish the chronological phases of the transition, which do not define the cultural phase, but they do help in understanding the dynamics of the same.

Taking this into account, the latest studies that have used only ^{14}C data, obtained analysing short live samples, have suggested that the Neolithisation of the Iberian Peninusla happened between 5,700 cal BCE and 5,500 cal BCE, and that it was a fast event that arrived into the interior parts of the Peninsula almost as fast as to the coastal zones (Alday, 2009; Bernabeu et al., 2011; Oms et al., 2014, 2016). Nevertheless, this last point is in debate, as many authors consider that some of the contexts from interior territories assignet to Early-Neolithic to be Mesolithic, indeed (García-Martínez de Lagrán, 2014, 2015, 2017). In any case, this has situated the beginning of the Neolithic in the Peninsula at the same moment as in Languedoc (in France) and Liguria (Italy). In fact, the neolithisation in the Northwestern area of the Mediterranean was influenced by two events (García Martínez de Lagrán, 2015). The first of the events, after 5,800 cal BC, is characterised by pottery with *Impressa-Ligur* style decoration (Bernabeu et al., 2011; Oms et al., 2014). These first Neolithic evidences are scarce, and related to an economy based on agriculture and livestock, dominated by herds of goats (*Capra hircus*) and emmer wheat (*Triticum disccocum*) crops. These archaeological sites are localised in zones near the Mediterranean Sea; both in Southeast France, represented by the cases of Peito Signado and Pont de Roque-Haute (Briois & Manen, 2009; Guilaine et al., 2017), and in the East of the Iberian Peninsula with the sites of Guixeres de Vilobí and El Barranquet (Bernabéu et al., 2011; Oms, 2014).

The second event was related to the presence of Cardial decoration in the pottery, and is documented after 5,600-5,500 cal BC (Guilaine, 2007; Oms et al., 2016). The sites that represent this moment are also found near the coastal and pre-coastal areas of the Northwest Mediterranean, and in isolated cases also in inland areas. At this time economy was dominated by the culture of naked wheat (*Triticum aestivun/durum*) and barley (*Hordeum vulgare*), and by herds of ovicaprids (*Ovis* and *Capra*) (Saña, 2013), while the bovine and swine domestication was still of little importance.

Nevertheless, whether this transition in the Iberian Peninsula happened by acculturation, population replacement or a heterogeneous model that involves both of them in different levels is still unclear. Furthermore, raw archaeological data is unable to shed much light onto this aspect, and bioarchaeological or anthropological analyses are necessary in order to get some answers.

1.1.1. The Upper-Palaeolithic and Mesolithic register in the Iberian Peninsula

The Cantabrian fringe, which mainly includes the coasts of Cantabria, Basque Country and Aquitania (France), is one of the richest territories in Europe regarding archaeological evidences of inhabitation during the Last Glacial Maximum (25,000-19,500 BP) and the Upper Palaeolithic (Figure 1). These evidences include habitation record, and outstanding rock art assemblages like those from Isturitz, Aitzbitarte IV, Amalda, Askondo, Arlanpe, Tercis, Mugarduia, Prado, among others (Garate *et al.*, 2014; 2015). Therefore, it has been proposed that this area, besides being a natural corridor for different animal groups in favourable conditions, was also a key refuge at the time the rest of Europe was covered in ice and the animal and human populations migrated to less unfavourable areas: the so called Franco-Cantabrian Refuge.

This abundance of sites and materials continued after the Glacial was over, during the Gravettian and Magdalenian (15,000-9,000 BCE), periods when Europe was again progressively repopulated from the glacial refugees. Concretely, the Magdalenian is very rich in this area, and starts to show more specialised societies depending on the resources surrounding them (Spikins, 2008). Some of the best known Magdalenian sites that present evidences of human activity include: Altamira, Aitzbitarte IV, Duruthy, El Castillo Ekain, Isturitz, Lumentxa, Praile Aitz, Santa Catalina, Santimamiñe, Urtiaga (Garate *et al.*, 2014). In addition, some isolated sites also appeared in Eastern areas of the Pyreneans, such as the Balma Guilanyà (Subirà *et al.*, 2009 a); and the Mediterranean coast such as Cingle de l'Aigua (Román-Monroig, 2010).

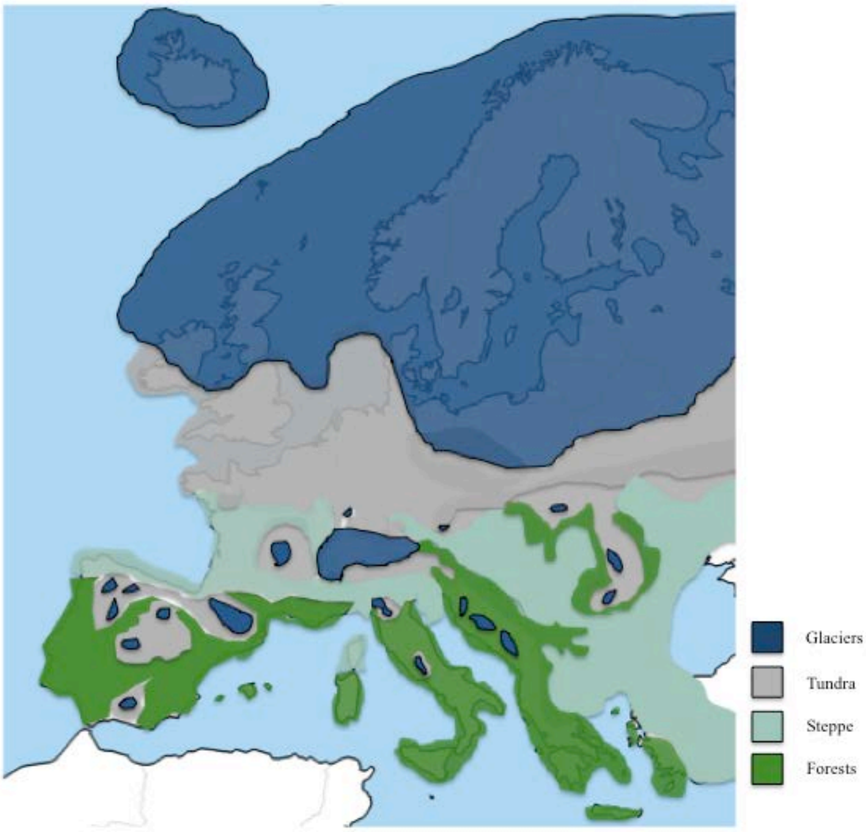

Figure 1. Map of Europe that represents the different climatic habitats during the Last Glacial Maximum (25,000-19,500 BP). (several sources)

The tendency during the Mesolithic was to craft smaller instruments than in the Palaeolithic and, although these societies would not have adopted agriculture or animal husbandry yet, they would be more specialised on the subsistence activities depending on the habitat. Therefore, we find specialised maritime seal-hunters, small groups in varied woodland environments.

As stated by Strauss (2008), most of the record for Mesolithic settlements and foraging adaptations is limited to coastal and near-coastal areas in the Iberian Peninsula. The main explanation to this phenomenon is that coastal habitats in the Holocene would be more favourable in resource availability than the interior and, therefore, human groups concentred in these areas.

In the Peninsular context, three types of Mesolithic industries, which happenned in different zones and chronology, can be detected (Barandiaran, 1998; Pluciennick, 2008; Strauss, 2008):

1. ‘Epipalaeolithic’: rich in backed bladelets and backed points with varying quantities of endscrapers and other Upper Palaeolithic tool types. Recorded during the Pre-Boreal Age, there are two branches of it.

    1.1. One of them was the Azilian, which includes bone industry. It is considered as the direct descendant of Magdalenian culture and it mainly developed in the Basque-Cantabrian zone.
    1.2. The other branch was the microlaminar ‘Epipalaeolithic’ industry, which lacks bone industry and is typically found in Portugal, Mediterranean coast of the Iberian Peninsula. This tradition also appears in Southwest France.

2. Geometric microlithic industries: appeared late in the Preboreal, and together with the macrolithic, it broke with the Upper Palaeolithic tradition. These representations are found in Northern Spain, Portugal and Mediterranean coast of the Iberian Peninsula. Moreover, they appear related to shell middens (concheros).

3. Macrolithic: dominated by cobble picks, choppers and /or large flakes, which can be found either essentially alone or associated with varying amounts of microliths. One of the most representative macrolithic cultures was the Asturian.

Besides this industrial diversity, the archaeological record shows how the areas were occupied and unoccupied in the different stages and the resources that were available in each zone and time. In Portugal the Preboreal period implies an increase in the number of sites and the diversity of the same, finding coastal shell middens like in Sintra Magoito (<10,000 BP), and open-air sites in the uplands like those found in Rio Maior. During the Boreal age there was an increase in the number of shell middens, which are basically found in the south and is a previous step to the zenith seen in the Atlantic Period, when most sites are coastal and estuarine (mainly in Sado & Muge). In the case of inland sites like ‘Forno da Talha’, where evidences of lithic raw materials obtenting and hunting have been found, evidences of connection with the coast have also been found (Strauss, 2008).

Although during the Pre-Boreal period coastal and inland areas were occupied in the Basque and Cantabrian area, and evidences show exploitation of marine, estuarine, riverine and big game resources; during the Boreal age there was clearing of inland territory, except in the Basque Country. In this concrete zone, evidences of hunting game from woodland areas and rocky slopes both near the coast and in the high, mountainous interior have been found. Eventually, in the Atlantic period the coast was still strongly occupied and the interior was reoccupied according to the findings in sites like Los Canes, Tarrerón and El Mirón (Apellaniz, 1971; Arias, 1991; Arias & Pérez, 1990; Straus & González-Morales, 1998).

In addition, the favourable coastal habitats with relatively rich and diverse resources allowed the last foragers to survive in the Atlantic façade of the Iberian Peninsula, while in the Mediterranean and interior areas the populations relied on food production economies. These latest hunter-gatherers would have lived between 7,000-5,500 BP, such as La Fragua, La Chora, Pico Ramos, Pareko Landa and Herriko Barra (González-Morales, 1995; López & Agirre, 1997; Mariezkurrena & Altuna, 1995; Zapata, 1995 a).

In the case of the Mediterranean coast of the Iberian Peninsula, the majority of known Early Holocene sites occur within 50 km of the present coast, and those that were not, are associated with lakes and lagoons, and the record is somehow scarcer than in the other two areas. Nevertheless, the oldest Mesolithic burials known to date, come from the Mediterranean area. Concretely, the oldest radiocarbon dates of the necropolis of El Collado go back to 9,475-9,300 cal BP (Gibaja et a., 2015).

1.1.1.1. Funerary record during the Upper Palaeolithic and Mesolithic

The funerary register found from the Upper Palaeolithic in the Iberian Peninsula basically consists of isolated or disturbed burials and bones with no anatomical connections. The best-known human remains from the late Pleistocene are found in Aitzbitarte, El Mirón, Erralla, Santimamiñe, Santa Catalina, Balma Guilanyà (Albisu *et al.*, 2014; Altuna *et al.*, 1985; Carretero *et al.*, 2015; Hervella *et al.*, 2012; de la Rúa & Hervella, 2011; Subirà *et al.*, 2009 a).

In contrast, during the Mesolithic repeated burials started to take place in different kinds of funerary sites, in the open-air, caves and rockshelters (Gibaja *et al.*, 2015). Nevertheless, as well as sites where more than two individuals are found, isolated burials in primary position are also found

(Figure 2). As it happens with the occupation evidences, these necropolises were located in three main areas: The Mediterranean coast of the Iberian Peninsula, the North of the Iberian Peninsula, and the Atlantic coast of Portugal.

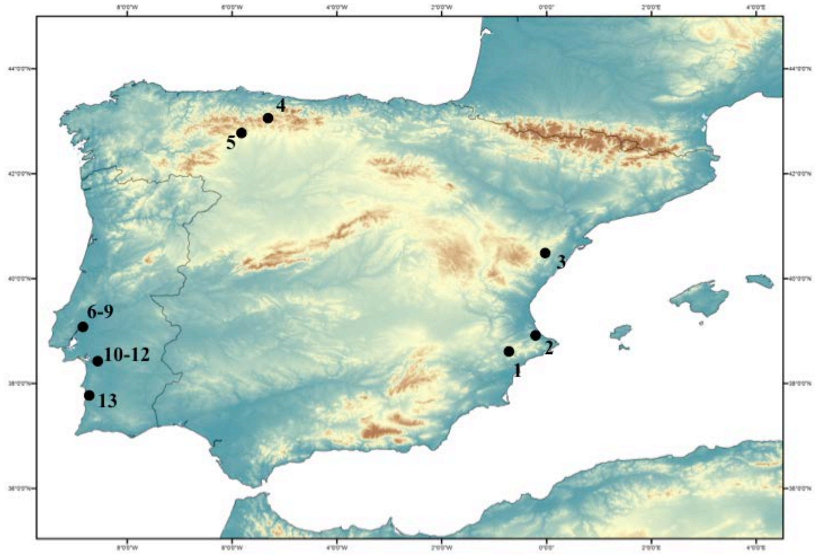

Figure 2. Mesolithic burials with more than two inhumated individuals. 1. Casa Corona, 2. El Collado, 3. Mas Nou, 4. Los Canes, 5. La Braña, 6–9. Muge Area (Cabeço da Amoreiras, Moita de Sebastião, Cabeço da Arruda, Cova de Onça), 10–12. Sado Area (Amoreiras, Arapouco, Cabeço do Pez), 13. Samouqueira. (Map generated by Gerard Remolins, Adapted from Gibaja *et al.*, 2015).

As it has been mentioned before the oldest evidences of Mesolithic burials are found in the Mediterranean area of the Peninsula. Some of the most representative sites are the rock-shelter of Mas Nou (Castellón) with 7 individuals, the cave of Santa Maria, the open-air site of Casa Corona (Alicante) with two burials, la Peña del Comptador (Alicante) also with two partial burials at the base of a long wall and especially the open-air site of El Collado (Valencia) with a necropolis with 14 graves, one of which contained remains of two individuals (Aparicio, 2008; Aura, 2010; Fernández-López *et al.*, 2013; Gibaja *et al.*, 2015; Olaria, 2010). As it has been mentioned before, El Collado presents the oldest evidences of Mesolithic funerary register, and the individuals from Mas Nou and Casa Corona were inhumated between 8,000 and 7,580 cal BP.

On the Atlantic coast of Portugal, the burials in the shell middens located on the estuaries of rivers Tagus and Sado have been known for long time. These contain remains of tens of individuals and are the largest human bone assemblages from the Mesolithic in the Peninsula. In the Muge area (estuary of River Tagus), for example, shell-middens like those of Moita de Sebastião, Cabeço da

Arruda and Cabeço da Amoreiras have surface areas of up to 3000 m^2 and a stratigraphic sequence nearly 5 m thick. The oldest dates of these assemblages are those obtained for Cabeço da Arruda that situates the first inhumates in 8,400-8,030 cal BP. On the other hand, the ^{14}C dates obtained for the sites from Sado estuary indicate that were used between 8,160 and 7,970 cal BP (Arias, 2013; Meiklejohn *et al.*, 2009).

Finally, the case in the north of the Iberian Peninsula (Cantabrian coast) is quite the opposite, and no large cemeteries have been recorded, mainly because the burials took place in small caves and rock-shelters. The best-known ones include: Cueva de Los Canes, Cueva de Los Azules, and shell midden J3 (Arias, 2007; 2013; Arias & Garralda, 1996; Fernández-Tresguerres, 1997; Iriarte *et al.*, 2010). Also in the north of the Peninsula, although not coastal, there are the burial of Abrigo de Aizpea (Barandiaran & Cava, 2001 a), and the two burials of la Cueva de la Braña and (Vidal & Prada, 2010). These burials date back to the period between 7,980 and 6,630 cal BP.

1.1.2. Neolithic in the North and Northeast of the Iberian Peninsula

The first evidences of domesticated plants and animals in the northeast of the Iberian Peninsula are registered once the Atlantic phase of the Holocene was fully established and stable, related to the *Impressa-Ligur* and Cardial cultures, which date back to the VI millennia BCE (Oms *et al.*, 2016). These first food producer societies were mainly associated with ovicaprine husbandry (*Ovis aries* and *Capra hircus*) (Tresset and Vigne, 2007; Vigne, 2007) and the domestication of barley and wheat (*Triticum aestivum t.compactum*, *Triticum aestivum/durum*, *Triticum dicoccum*, *Hordeum vulgare nudum* and *Hordeum vulgare*), (Antolín *et al.*, 2015; Zapata *et al.*, 2004). Nevertheless, evidences of the domestication of beans (*Vicia fava*) and peas (*Pissum sativum*), as well as husbandry of oxen (*Bos taurus*) and pigs (*Sus domesticus*) are present in sites like La Draga (Antolín & Buxó, 2012; Saña, 2011).

Usually, the presence of pottery is related to the domestication of vegetal and animal species, although it has been proposed that some sites representing hunter-gatherer cultures would have presence of ceramic vessels, obtained by trade from producer groups (Alday, 2009; Straus, 2008).

The first type of ceramic introduced in a generalised way into the Iberian Peninsula is the Cardial one, which spread through the Mediterranean coast and the Portuguese part of the Atlantic Façade, and soon enough in the interior areas of influence of the previous ones (Oms *et al.*, 2016) (Figure 3).

These first farmers inhabited caves, such as Can Sadurní, Chaves, Cova Bonica (Oms *et al.*, 2016), where evidences of habitation in the form of tool crafting residues, animal bones, seeds and pottery coexist with funerary manifestations. Nevertheless, in recent evidences of open-air habitation sites have also been found. The most representative of these open-air sites are the lacustrine village of La Draga (Gerona) (Bosch *et al.*, 2011), Plansallosa (Gerona) (Bosch *et al.*, 1999), and Los Cascajos and Paternanbidea (Navarre) (García & Sesma, 2001, 2007). This was the first step of a gradual adoption of life in open-air villages like those found at the Ebro basin and during the Middle Neolithic Age in Catalonia. Moreover, the populations would increasingly occupy valleys and lowlands as the groups grew demographically and the needs for natural resources increased. This process would take a foothold during the Middle Neolithic Age and continue on towards the Bronze Age. It would also be related to an increase in the presence of structures aimed to store grain (Albizuri *et al.*, 2011; Alonso, 1999; Bouso *et al.*, 2004).

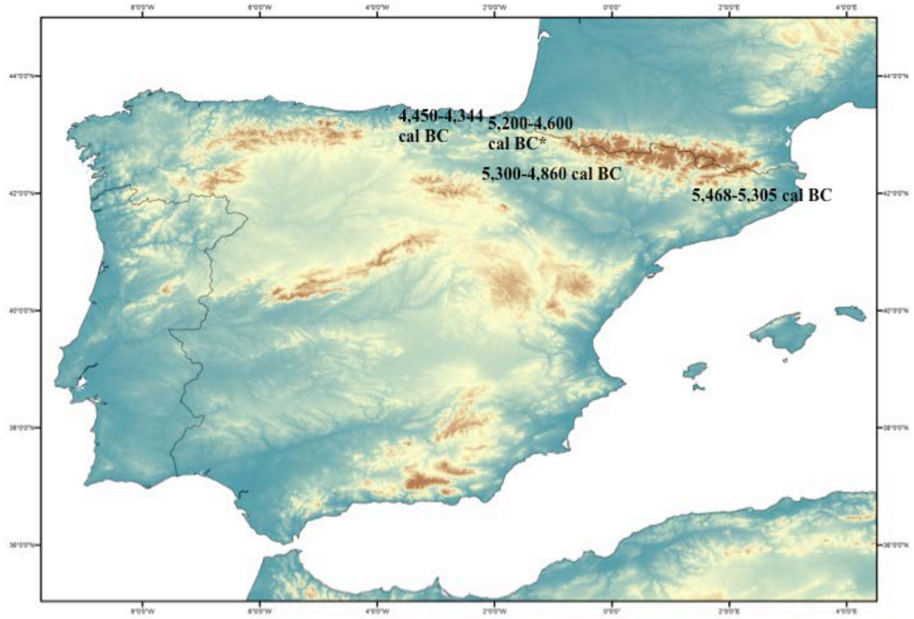

Figure 3. Oldest representations of domesticated vegetal species in the Northeast of the Iberian Peninsula. The data have been obtained from: Fernandez-Eraso *et al.*, 2014; Oms *et al.*, 2016; Peña-Chocarro *et al.*, 2005; Zapata, 2005). *This sample has not been obtained from a cereal grain as the rest, but from cereal polen from Herriko Barra site. (Base map generated by Gerard Remolins).

The Neolithic spread at different times and representations in the various zones from the northeast of the Iberian Peninsula. Overall, it can be divided in some chronological and cultural periods that facilitate the organisation of the archaeological evidences recorded (always keeping in mind that there might be exceptions). This division is based on data from the richer zones of Catalonia and the Ebro basin (Oms *et al.*, 2016):

1. Early Neolithic: 5,500-4,000 cal BCE. The first extended productive societies were related to the *Impressa-Ligur* and Cardial pottery, and for this reason the first part of the age is called Cardial Early Neolithic: 5,500-4,850 cal BCE. This phase is characterised by the presence of pottery mainly decorated with impressions of *Cerastoderma edule* and *Cerastoderma glacum*. It concentrates mainly near the Mediterranean coast, precoastal and inland territories around the Pyrenees. (Chaves, Layer C18 of Cova de Can Sadurní, Cova Foradada, La Draga, Peña Larga, Plaça de la Vila de Madrid, Balma Margineda).

2. Middle Neolithic: 4,200-3,100 cal BCE. This phase was characterised by the blossom of funerary practices, and most knwoldege is due to the sutdy of the sepultures. Some of the most representative sites from this period correspond to the *Sepulcres de Fossa* culture (Pit Burial),that includes Burials in Pits in valleys and coastal areas from the region that nowadays is Catalonia, and Stone-Cist from Pre-Pyrenean and Pyrenean areas. For example, we can mention Bòbila Madurell-Can Gambús, Camí de Can Grau, Feixa del Moro. The pottery from these sites was generally smooth, with careful finishes and composite profiles, usually carenated.

3. Late-Neolithic and Chalcolithic: 3,600-2,300 cal BCE. During this phase most burials were collective, mainly in caves and evidences suggest that the exchange networks changed.

In a Western European context, the first contexts showing Cardial pottery produced similar ^{14}C dates to the Provençal and Lower Rhône's sites (Barceló, 2008). In some areas we can distinguish concrete phases of the Early Neolithic that were not cardial but can be grouped in a common cultural manifestation. These were clearly observed in the Mediterranean area of the Iberian Peninsula.

On one hand, there was the Epicardial Early Neolithic, which took place around 4,800-4,560 cal BCE. This phase is related to the expansion of two different decorative traditions on the pottery (one that is recognised by a smooth orthogonal cordon, while the other combines incisions and impressions). Representations of this phase have been recorded both in caves and in the open air (Ca l'Estrada, Cova de l'Avellaner, Plansallosa). On the other hand, there was the Postcardial Neolithic (Molinot and Montboló Groups), around 4,690-3,800 cal BCE and was more concentrated in the mountainous regions.

During this first phase of the Neolithic evidences are found both in caves and open-air sites. In the Northeast of the Peninsula the main exploited animals were ovicaprids and oxens, while suides were sometimes found, but not always. Moreover, ovicaprid husbandry was more common in caves and rock-sheltters, while the presence of oxen was predominant in open-air sites (Bosch & Tarrús, 1990; Martín, 1992; Nadal *et al.*, 1999; Saña, 1997). The presence of wild animals was scarce in most contexts; thus, it was more common in caves (Albizuri & Nadal, 1993; Saña, 1997). Moreover, according to the register of the age-at-death of the animals, these were mainly raised for meat production (Saña, 1997). In this period, the origin of most lithic raw materials was local. The exception is found in La Draga, where most of the used flint was exogenous (Gibaja & Clop 2012).

Therefore, it is clear that the first representations of the Neolithic occurred in the Mediterranean area and the middle Pyrenees. Nevertheless, the detection of Neolithic evidences on the Atlantic coast has increased in the last few years, and these have shed some light onto the earliest examples of the same in that area (Fernández-Eraso *et al.*, 2015; Fano *et al.*, 2015). While it was believed that the establishment of a producer culture started in an advanced stage of the Neolithic period and mainly by the adoption husbandry and not agriculture, the discovery of barley and coated wheat in caves such as El Mirón (Cantabria), Lumentxa, Kobaederra and Pico Ramos (Basque Country) and cereal polen in Herriko Barra (Basque Country) situate the beginning of the agriculture around the end of the VI millennia and beginning of the V BCE (Peña-Chocarro *et al.*, 2005; Zapata et al., 2005). In parallel, the Early Neolithic town of Los Cascajos (Navarre) presented evidences of cereal harvesting and the radiocarbon dates the first occupations 5,310-4,974 cal BCE (human bone) (García-Gazolaz *et al.*, 2011).

During the Middle-Neolithic the caves and rock-shelters were mainly abandoned in the Northeast, as valeys and plains became the preferred habitation areas. This change was related to an active selection of more fertile soils to improve the profit of agriculture and animal herding (Ribé, 1996). Due to this new location, we get most of the information about these groups from negative structures (ditches, silos and graves) (Terradas *et al.*, 2016). In the sense that the representation of strong funerary cultures developed at this time, most of the information sourrounding the Middle-Neolithic in the Northeast of the Iberian Peninsula provides from these contexts. The amount of domesticated vegetal and animal especies increased in this period as farming was the main economic activity (Gibaja & Clop, 2012). The recovered pottery was smooth, like that from other areas of the west Mediterranean at the same period (Martín & Tarrús, 1991). As it will be mentioned later, the culture present in the Northeast of the Iberian Peninsula presented many affinities (funerary practices and raw materials) with other cultures from Western Europe, and especially with the Chasséen in France (Gibaja *et al.*, 2013; Molist *et al.*, 2016; Terradas *et al.*, 2014, 2016).

During the Middle-Neolithic and Late-Neolithic/Chalcolithic the occupation and funerary record spreads through all the Northeast and North of the Iberian Peninsula, although there are differences in the diverse areas, mainly captured in the funerary record. The new studies have shown that the first megalithic evidences in the Basque Country, in opposition to previous believes, appeared in the Middle-Neolithic age (both in the Cantabrian fringe and the most Mediterranean area), which include assemblages like San Martín, Los Llanos, Kurtzemendi, La Cabaña 2, Katillotxu V, Boheriza, Otsaarte and Trukuaizti II (Fernández-Eraso *et al.*, 2015). This situates the beginning of the phenomenon in similar chronological phases as it happened in the Eastern areas of the Pyreneans (Martin & Tarrús, 1994; Tarrús, 2002).

1.1.2.1. The funerary record and its evolution

The funerary practices during the Neolithic in the northeast of the Iberian Peninsula were diverse, depending on chronology and geographical area. These practices are a great source of information for the researchers in many aspects. The principal one is that the funerary contexts provide the only remains that can be analysed in order to get direct biological and health-state data about the populations and their individuals: human bones. Moreover, the differences in the way the dead bodies were treated and the manifestations might indicate distinct traditional origins. Finally, in some cases the inhumation structures are a great source of artefacts that were deposited, such as grave-goods. These can be analysed in order to determine the production techniques, origin of raw materials, etc.

During the Early Neolithic Age (VI-V millennia BCE) the funerary register is scarce both in number of sites and inhumated individuals. Those burials would take place in caves and rockshelters at first, like the case registered in the caves of Chaves, Can Sadurní, Cova Bonica and Cova Foradada, which are related to the Cardial culture (Oms *et al.*, 2016; 2017). In these caves the archaeological records indicate that the inhumations took place simultaneously to the same ones being inhabited. The first open-air burial is also registered in this incipient phase of the Neolithic, the Pit-Burial of Plaça de la Vila de Madrid (Barcelona) (Pou *et al.*, 2010).

Further north, through the Ebro valley in Navarre, there is evidence of two sites with burials from the Early Neolithic that belong to the late VI millennium BCE and beginning of the V millennium BCE. The two of them, Los Cascajos and Paternanbidea, present several excavated negative structures (pits) where one individual (occasionally two) was buried, similar to the isolated structure found in Plaça de la Vila de Madrid (Barcelona). In fact, although burials in caves and in the open-air coexisted during all the Early Neolithic, as long as this period advanced in time a major number of burials happened in open-air and the ones in caves got reduced (Oms *et al.*, 2016).

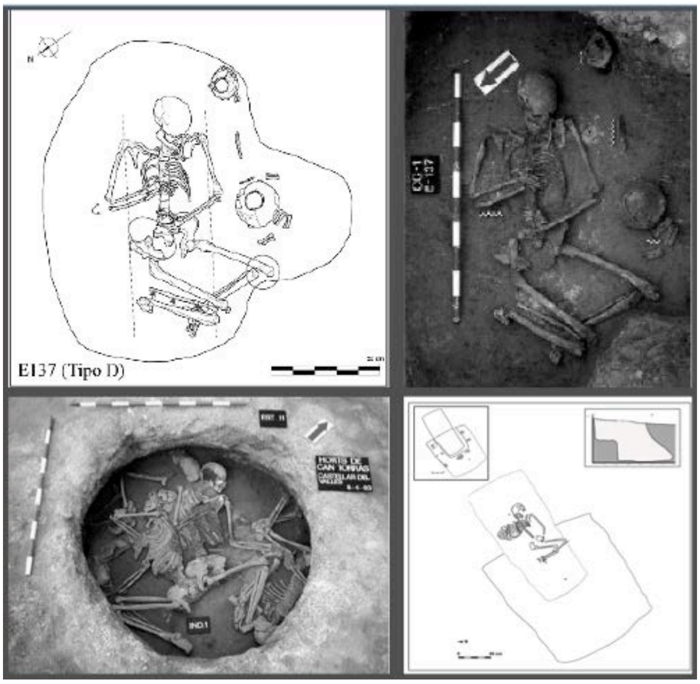

Figure 4. Examples of different burials corresponding to the Sepulcres de Fossa Culture. Upper row: scheme and photography of structure E137 from Can Gambús (Roig et al., 2010). Lower row: structure E11 from Horts de Can Torras (left) (Coll & Roig, 2005); and scheme of structure E33 from Camí de Can Grau (right) (Martí *et al.*, 1997).

During the Middle Neolithic (final V millennium and initial IV millennium BCE), the open-air funerary practice got consolidated and presented its maximum expression (Gibaja, 2004 a). Nevertheless, although to date, the best-known funerary culture of this period is the so-called ‘Sepulcres de Fossa’ culture (Pit burial culture) (Bosch-Gimpera, 1923-1924) there were also different expressions in different areas. The Sepulcres de Fossa were mainly dominant in the Mediterranean coastline and pre-coastal areas, as well as in the inner valleys. Like the previous open-air burials, these consisted of pits excavated in the soil containing one or two individuals (Figure 4). Thus, in this period some of these pits had lateral chambers and were closed with big gravestones or wooden trunks (Gibaja, 2004 a), and compared to the previous phases they tend to appear grouped. Some of the best examples of this culture are the necropoles of Bòbila Madurell/Can Gambus, Sant Pau del Camp or Puig d'en Roca. This culture has been compared to the Chaseen in southern France because of the many similarities that they share (Vaquer, 1990).

Usually, these burials contained a single individual: man, woman, or child. In some concrete cases though, the structures enclosed two, and three or more individuals. In most cases, the burials were in primary position, and presented anatomical connection between the bones, although in isolated cases the bones had been displaced towards the sides of the grave to make room for new burials. Recent studies on funeral taphonomy have provided important information about certain aspects that had not been treated so far. For example, today we know that these individuals were not simply deposited in the bottom of the funerary structure, but occasionally placed in the interior of the tomb within rigid boxes, probably wooden, or in bags (Allièse *et al.*, 2014).

In the region that today is known as the Solsonès (Catalan pre-Pyrenees) and Andorra a different manifestation, although included in the *Sepulcres de Fossa*, is recorded for the burials during the Middle-Neolithic Age. These burials were done in tombs created with stone slabs, called cists (Figure 5). These structures generally had an opening in one side and were habitually sealed with a little tumulus. In the same way as it occurs in the Sepulcres de Fossa culture, each tomb usually contains one or two individuals, although there are exceptions like in the case of el Solar III, where three individuals were buried, and in Costa dels Gàrrics de Caballol the number of individual is seven. In addition, most of the structures are found isolated, but in a few cases they were grouped together forming little necropolis like the nine sepulchres of el Llord and the five of el Solar (Cardona & Guàrdia, 1995; Castany, 2008; Serra Vilaró, 1927).

Moreover, Martín and Tarrús (1994) and Tarrús (2002) have documented dolmenic funerary structures in l'Empordà region that correspond to the IV millennium BCE, although the many natural and anthropic alterations that these have suffered makes it difficult to ascribe them to a concrete chronology and characterise both the burial and the materials (Gibaja, 2005). Similar semi megalithic tombs are also found in the Chaséen site of Le Crés (Loison *et al.*, 2004; Loison & Schmitt, 2009).

The situation in the Basque zone (Araba, Bizkaia, Gipuzkoa and Navarre) diverges from that described for the remaining territory. On one hand the record corresponding to Middle-Neolithic (late V millennium and IV millennium) burials is scarce. And on the other hand, the number of sites with ^{14}C dates in short life materials is also low. Therefore, according to the literature, most funerary sites correspond to late phases of the Neolithic Age (adanved IV millennium) and to the Chalcolithic (second half of the IV millennium).

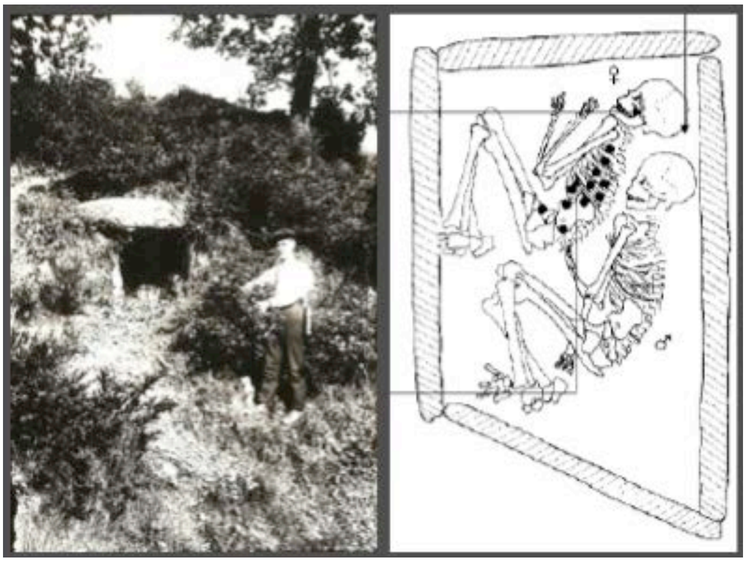

Figure 5. The cist of El Llord III, external photography and scheme of the internal findings. (Photography: Museu Diocesal i Comarcal de Solsona; Scheme: Castany, 2009).

The continuation of utilisation in Los Cascajos during the Middle Neolithic also presented burials in pits excavated in the soil, although these are not included in the Sepulcres de Fossa culture. Only Ekain, Lumentxa and Marizulo present burial records from the Middle Neolithic in the Atlantic basin of the Basque Country to date (Arribas, 2015 personal communication; Basabe 1971; Mariezkurrena, 2014 personal communication). All three were burials in caves, although the individual from Marizulo was inhumated in a cist-like semi-megalithic construction inside the cave (Laborde *et al.*, 1967). Some authors (Fernandez-Eraso *et al.*, 2015; Strauss, 2008) assign the first Atlantic megaliths to this period, starting in the east with the examples of: Larrate, Trikuaizti II, Otsaarte and Katillotxu V.

During the late Neolithic and Chalcolithic most funerary representations were collective burials that either took place in caves or megalithic monuments. In the case of the caves, many of them that had lost their functions after the Postcardial Neolithic, at that moment recovered it for the funerary purpose (Armendáriz, 1990; Armendáriz & Etxeberria, 1983; Martín, 2003). Moreover, other smaller caves that were not suitable for inhabitation were used for this funerary purpose too. In the case of the Megaliths, the ones from the Basque Country are the most controversial. As I have mentioned before, it could be due to the shortage of high quality chronological data. This merges with a poorer preservation of the remains of the Megaliths from mountainous areas.

In any case, the situation in the Basque Country is that two groups of monuments can be differenciated, the ones that appear in the Atlantic side's mountains and those from the inner valleys (Armendáriz, 1987; Andrés-Ruperez, 1990). The former are usually dolmenic structures with small and simple floors (Figure 6), while those from the valleys are usually corridor sepulchres and present rich collections of grave-goods.

Therefore, there are still doubts about the origin of megalithism in the area and whether the two branches had different origins, or that one is an evolution of the other. Most of the dated samples are charcoals, which in many occasions give inaccurate and too old dates, and they do not differ between the two areas. Nevertheless, the last works situate the origin of both Atlantic Basque Country's and Mediterranean Basque Country's megaliths in the Middle Neolithic age with a few representations in both areas (Fernandez-Eraso *et al.*, 2015).

Finally, the grave-good analysis suggest that in the Basque area, caves started to be more intensely exploited for funerary purposes in a late phase of megalithic use, although it seems that the two practices coexisted for a time (Ontañon & Armendariz, 2005). Recent studies analysing the demographic patterns of both burial typologies show no differences between them, which excludes theories suggesting a preferential burial of concrete social groups in the megaliths compared to caves (Fernandez-Crespo & de la Rúa, 2016).

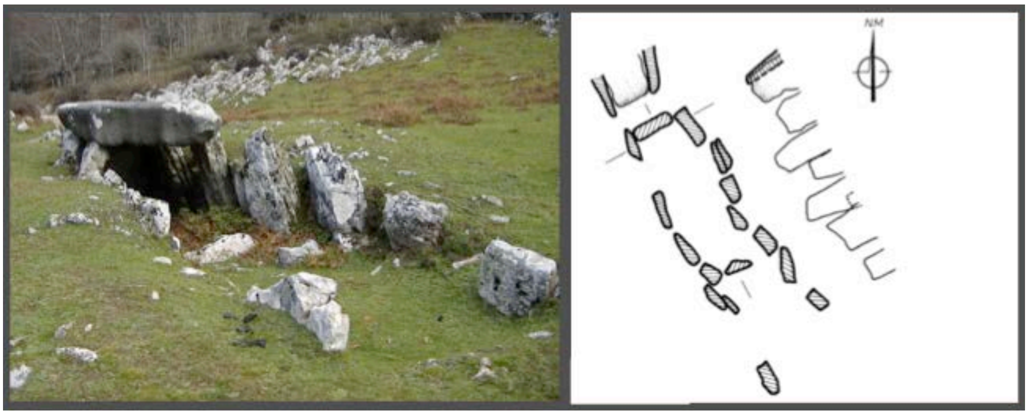

Figure 6. Phtography and scheme of Jentilarri megalith, one of the best preserved from the mountaneous area of the Basque Country. (Photography: Mujika & Edeso, 2012; Scheme: Apellaniz, 1973).

1.1.2.2. Exchange networks, the evidence on raw materials

The analyses on the mineral materials found in the archaeological contexts allow the establishment of their origin. In this sense, the analyses on flint and different kind of lithic materials, like variscite and obsidian, shed light on the goods-exchange networks present at the different periods.

Two main networks have been proposed and investigated for a long time. On the one hand there is one that runs through the Ebro river's valley, Northwest to Southeast and *vice versa* (Baldellou *et al.*, 2011; Cava *et al.*, 2008; Montes & Alday, 2011; Tarriño & Terradas, 2013); on the other hand, a transpyrenean network seems evident, with interactions between groups from both sides, this, according to the material record was more intense in the Mediterranean area (Gibaja *et al.*, 2013; Terradas *et al.*, 2011; Terradas *et al.*, 2014). Moreover, the summit of these networks occurred during the Middle-Neolithic, once the patterns that started to develop during the early phase of the Neolithic period were completely established (Oms *et al.*, 2016).

In this context, regarding the Ebro's networks, Variscite from Gava's Can Tintorer mines appears in sites such as Paternanbida (Navarre), Cueva de Chaves and Cueva del Moro de Olvena (Huesca) (Baldellou *et al.*, 2011). Moreover, although most of the flint used in the Cantabrian area during the Neolithic was from a local origin, between 1 and 10 per cent of the material was Evaporitic flint from the Ebro's basin (>100 Km), and around 1% came from further areas (>200-300 Km) (Tarriño & Terradas, 2013).

On the Mediterranean area of the Iberian Peninsula, Barrémo-Bédoulian flint (honey flint) from Vauclase (Provence, France) has been identified in several sites from both the pre-Pyrenean zone and related to cist-like toms, and in pit burials from the plains (Binder, 1998; Briois, 2005; Gassin *et al.*, 2011; Gibaja *et al.*, 2011, 2013; Léa, 2004). The probable origin of this flint was as far as 450 Km away from some of the sites that it has been found in. Moreover, polished axes originated in the Alps (Léa, 2005; Pétrequin *et al.*, 2012; Vaquer *et al.*, 2011), and Obsidian blades and cores from Sardinia have also been found (Gibaja *et al.*, 2013; Terradas *et al.*, 2014). Nevertheless, the presence of these obsidian artefacts was scarcer than in archaeological sites from Southern France. The period of most intense activity occurred during the IV millennium BCE. The sense of the exchange networks was not only east-to-west, as it is evidenced by variscite pieces originated in Gavà (Barcelona) that have also been found in the Rhone's valley. However, this exportation of the minerals occurred with posteriority to the main explotation moment of the mines (Terradas et al., 2016). Moreover, exchanges regarding variscite and diverse flint kinds between valley and mountainous areas have also been documented in the Catalan area (Bosch & Borrel, 2009; Villalba *et al.*, 1986).

Nevertheless, during the Late Neolithic and the Chalcolithic the evidences on the Mediterranean exchange network disappeared or decreased in the archaeological register, as no obsidian or Vauclase's honey flint were present in the Iberian area (Oms *et al.*, 2016). It does not mean though, that all the raw materials have a local origin, because as the studies in sites like Cova del Pantà de Foix show, two flint blades have been identified from the Provence area (Folcalquier) in southern France (Cebrià *et al.*, 2013). In addition, in the collective burial contexts from the Solsones area (Catalan Pre-Pyrenees), an important portion of the flint had its origin in the middle Ebro basin (>250 Km away). Finally, Tarriño and Terradas (2013) also observe flint movements in the northern area, basically of that from the Flysch area and those that originated in the Ebro basin.

1.2. GENETIC STUDIES ON THE ORIGIN OF THE NEOLITHIC HUMAN POPULATIONS AND THEIR DIVERSITY IN EUROPE AND THE IBERIAN PENINSULA

Together with the Middle Palaeolithic colonisation of Europe by *Homo sapiens* and the posterior re-expansion of human groups after the Last Glacial era, the Neolithisation has been proposed as the main genetic shaper in European human groups (Hervella, 2009). Due to this fact, several genetic analyses have been focused on trying to elucidate how the process occurred by analysing classical genetic markers in modern Europeans, mitochondrial DNA (mtDNA) in both modern and ancient populations, Y chromosome analysis, and more recently genome-wide analyses in ancient samples (Achilli *et al.*, 2004; Ammerman & Cavalli-Sforza, 1984; Baleresque *et al.*, 2010; Behar *et al.*, 2013; Cardoso *et al.*, 2011; de la Rúa *et al.*, 2015; Szécsény-Nagy *et al.*, 2017). The origin of the first agricultural societies is widely accepted to be in the Near-East, and according to the cultural records, there are two main routes of dispersion in Europe: The Mediterranean route, which is related to the Cardial pottery and goes east to west; and the Danubian route, related to the LBK culture and its record expands south to north in central and eastern Europe (Thorpe, 1996).

The first studies on classical genetic markers in current European populations included Human Leukocyte Antigen (HLA) system's loci, genes that determine the blood groups and diverse plasmatic enzymes and proteins (Menozzi *et al.*, 1978), and were then expanded on in different studies (Ammerman & Cavalli-Sforza, 1984; Cavalli-Sforza *et al.*, 1993; Piazza *et al.*, 1995; Sokal *et al.*, 1991). These analyses showed some gradients and clines for the markers, and the most important is that represented by the first Principal Component (30% of the total variability). This component presents a southeast-northwest gradient that would coincide with a population migration from the Near East towards the west.

In contrast, the first mtDNA analyses in modern populations show different results. The analysis of many European and Near-Eastern populations, together with the application of new methodologies to estimate the origin of concrete mitochondrial linages and haplotypes (TMRCA and Founder Analysis, for example) suggest that the majority of the genetic diversity in the female lineage of current European populations is originated in the Palaeolithic colonisation of the continent (Macaulay *et al.*, 1999; Richards *et al.*, 1996; 1998; 2000). According to these authors, no more than 23% of the genetic variability of present-time Europeans can be traced to the Neolithic expansion. Concretely, in the Mediterranean zone this proportion would be between 9-12%, and 15-22%, sensibly superior, in central Europe. Moreover, analyses focusing on the frequency and distribution of V, H1 and H3 haplogroups of the mtDNA suggested that these families were present in Europe during the Upper Palaeolithic and underwent a new spread episode from the Cantabric Fringe at around 11,000 BP (Achilli *et al.*, 2004; Torroni *et al.*, 1998, 2001).

Regarding the Y chromosome studies, there are different interpretations, as there appears a gradient similar to that found in the analysis of the classical markers (Roser *et al.*, 2000; Semino *et al.*, 1996; 2000) that would indicate the expansion route for the Neolithic groups. Moreover, Balaresque and collaborators (2010) identified haplogroup R1b1b2 as the predominant Y chromosome haplogroup in Europe, and they also determined that it presents an East to West gradient, which indicates that the paternal lineage is predominantly of European origin in Europe. Nevertheless, in other studies R1b has been identified more commonly in Western Europe, concretely the Iberian Peninsula and British Island and Ireland, while in Eastern Europe R1a is predominant (Wiik *et al.*, 2008), which might be related to the Post-Glacial expansion of populations from the Franco-Cantabrian Refuge.

In any case, what in the beginning of these kinds of studies seemed to be an easy question to answer has proved to be more complicated. These initial studies indicate that the process was neither homogeneous nor simple, and proved the necessity of regional analyses as well as ancient DNA (aDNA) studies. In this sense, one of the most intensely studied population from western Europe is the Basque, mainly incited by its cultural uniqueness in the area, being the only group in the west of the continent that speaks a non-Indoeuropean language, Euskera, as its most peculiar feature. The uniqueness of the genetic diversity in this population has been reported in many works based in in classical markers (Cavalli-Sforza & Piazza, 1993), autosomic STRs (Short Tandem Repeats) and SNPs (Single-nucleotide Polymorphisms) (Bauduer, 2017; Rodríguez-Ezpeleta *et al.*, 2010) and mtDNA (Behar *et al.*, 2012; Cardoso *et al.*, 2011; 2013; Wilson *et al.*, 2001). Nonetheless, studies analysing inmunoglobulines (Esteban *et al.*, 1998; Giraldo *et al.*, 2001) and autosomic and Y chromosome markers (Calderón *et al.*, 2000; 2003; Laayouni *et al.*, 2010; Peña *et al.*, 2002; Wilson *et al.*, 2001) have suggested that the diversity of the Basque population is not that different from the surrounding populations, and that it neither presents greater genetic differences with other groups than the normal found in the area. These data, although controversial, shows at least, that maybe the maternal and paternal lineages had different dispersion patterns.

Some authors have attributed the differences the current-time Basque population presents to cultural diffusion of the Neolithic in the area, which implies that the genetic background of the Basque populations would be of a Pre-Neolithic substrate (Behar *et al.*, 2012; Cardoso *et al.*, 2011; 2013; Cavalli-Sforza & Piazza, 1993). Other authors attribute the extreme frequencies observed in some markers in the Basque population to the genetic drift posterior to the expansion of the agriculture in the area (Richards *et al.*, 2000; Rosser *et al.*, 2000).

Therefore, in order to determine the origins of current genetic diversity in the different populations it is necessary to analyse the composition of previous populations. The results that include various European areas suggest differential patterns along the continent: while in central and eastern Mediterranean a clear genetic influence that originated in the Anatolian region has been registered (Haak *et al.*, 2015; Hofmanová *et al.*, 2016), this influence is not present in the Baltic area (Jones *et al.*, 2017). Moreover, in the northern fringe Malmström and colleagues (2015) found that the Neolithic samples differ from the previous hunter-gatherers of the zone and share a close affinity to Central European farmer populations. Finally, in the west of Europe (including the Iberian Peninsula) the process seems to be more complex, with different signals of incoming populations in the areas and through the whole Neolithic period (Hervella *et al.*, 2012; Pereira *et al.*, 2017; de la Rúa *et al.*, 2015; Sampietro *et al.*, 2007; Szécsényi-Nagy *et al.*, 2017).

Concretely, in their 2012 work, Hervella and collaborators suggested that small incoming groups would randomly affect the composition of the autoctonous populations in the development of the Neolithic in the Iberian Peninsula, in contrast to the clear signals observed in other continental areas. This suggestion was elaborated from the results of their work and from those by Sampietro and collaborators (2007), where they detected more intense signals in the Mediterranean coast of the Peninsula. New studies suggest that the Early Neolithic samples from the Cantabrian fringe do not present differences with the previous hunter-gatherers, and that they presented low frequencies for haplogroups J and U of the mtDNA in contrast to most eastern populations (de la Rúa *et al.*, 2015).

Nevertheless, the Chalcolithic populations differed from the Early Neolithic ones in the fringe, being more similar to those from the Mediterranean areas, which could be indicative of post-Neolithic population relationships or demographic events. In addition, the genome-wide sequence data of Chalcolithic individuals from El Portalon cave (Sierra de Atapuerca) have shown affinities between them and modern-day Basques (Günther *et al.*, 2015). Moreover, the mtDNA and Y chromosome haplogroup composition of these individuals is also consistent with an admixture between incoming farmers and local hunter-gatherers. In fact, Szécsényi-Nagy and collaborators (2017) observed that there were no genetic differences between Middle-Neolithic and Chalcolithic samples in the Iberian Peninsula. Moreover, they also observed that these samples from advanced periods of the Neolithic (IV millennium BCE) were genetically more similar to Iberian Hunter Gatherers than most samples from the Early Neolithic.

Finally, overall in Europe there is a genetic change in advanced stages of the Neolithic age, which seems to be related to the expansion of the Corded Ware people. Their ancestry can be traced on a 75% level to the Yamnaya steppe herders from Russia (Haak *et al.*, 2015). Moreover, the authors suggest that this group would be on the base of the dispersion of the Indoeropean languages, as they migrated in an advanced phase of the Neolithic. In contrast, researchers do not find this steppe signal in samples from the Iberian Peninsula (Olalde et al., 2017), which might be related to the previously mentioned continuity from the Middle-Neolithic to the Chalcolithic in the population composition, and it would also continue during the Bronze Age.

1.3. TEETH: STRUCTURE, DEVELOPMENT AND THEIR STUDY

Teeth are the best-preserved and the most abundant human remains in the majority of archaeological and paleontological sites. Therefore, it can be considered that the fossil history of dental remains is more complete than those of other anatomic entities. This occurs due to a combination of two main factors. On one hand, the outer layer of teeth, enamel, is the hardest tissue in the body, as it is mainly (95-96%) of inorganic origin; concretely calcium hydroxyapatite [$Ca_{10}(PO_4)_6(OH)_2$] (Nanci, 2008; Simmer & Fincham, 1995). On the other hand, excluding rare cases of anodontia, all humans in all places and times had, have or will have teeth (Scott & Turner, 1997).

In the following sections I will provide some basic information on human dentition and teeth in order to get a better understanding of this first statement.

1.3.1. General concepts of human dentition and the anatomy of human teeth

Human dentition is diphyodont because it presents two sets of teeth (Figure 7). These are the decidious one (or milk dentition) and the permanent dentition, which systematically replaces the former. Two arcades compose each of the dentitions: the upper arcade (maxillary) and the lower arcade (mandible). Each of them is divided in two quadrants: right and left. Therefore, we define four quadrants in the dentition: upper right, upper left, lower left and lower right. The median sagital line of the skull separates left and right quadrants, so they are mirrors.

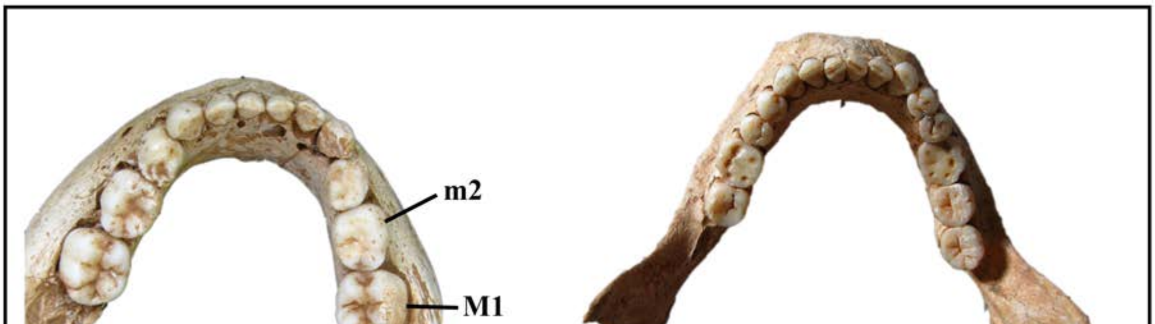

Figure 7. Decidious (left) and permanent (right) human mandibular dentitions.

As humans are also heterodont (like all mammals), each quadrant is composed by morphologically diverse teeth. Humans present four kinds of teeth: incisors, canines, premolars and molars. Each quadrant of the deciduous dentition is formed by two incisors, a canine and two molar-like premolars. Usually, these premolars are referred to as molars in human dentition, as the tradition comes from dentistry. Nevertheless, from an evolutionary point of view, they are the third and fourth deciduous premolars (Hillson, 1986). Meanwhile, two incisors, a canine, two premolars and three molars form the permanent dentition.

Incisors have a flat and blade like crown and they locate in the central zone of the arcades. The main reason why they are so compacted is because, besides cutting, they share the function of ripping and tearing food off with canines. Canines have conical crowns. Premolars present a transitional form between canines and molars. Usually they have two cusps, and their crowns are round, shorter than canines, and smaller than molars. Molars are located in the posterior zone of the arcades, and have large, square-like crowns, and bear more cusps than any other tooth. Their function is to grind and chew food.

Table 1. Dental nomenclature used by the FDI system and palaeontological notation for permanent teeth.

		FDI system		
		Right		Left
UPPER JAW	UI1	11	Incisors	21
	UI2	12		22
	UC	13	Canine	23
	UP3	14	Premolars	24
	UP4	15		25
	UM1	16	Molars	26
	UM2	17		27
	UM3	18		28
LOWER JAW	LI1	41	Incisors	31
	LI2	42		32
	LC	43	Canine	33
	LP3	44	Premolars	34
	LP4	45		35
	LM1	46	Molars	36
	LM2	47		37
	LM3	48		38

From the many nomenclature systems used in the literature, the one chosen for determining the concrete pieces in this study is the FDI system that gives two numbers to each tooth (Table 1). The first one defines the arcade (either decidual or permanent), while the second one defines the position of the teeth in the arcade (1 to 8 starting in the first incisive and finishing in the last molar). Moreover, when referring to the teeth class -with no regards to laterality- I have used a paleontological nomenclature where: I/i refer to incisors; C/c to canines; P to permanent premolars; and M/m to molars (including decidual premolars, in order to follow with the literature's tradition in human remains). Before these letters a "U" is added for upper teeth and "L" for mandibular ones and a number for the position regarding the tooth class.

Some basic terms on dental anatomy are necessary in order to functionally understand the descriptions and work with methodological consistency in dental anthropology.

The mesial side of a tooth is the one closest to the point where the central incisors contact each other, and distal is the opposite to it. The lingual portion of a tooth is the one that is towards the tongue. Labial (incisors and canines) and buccal (premolars and molars) are the opposite sides to lingual, although vestibular can also be applied. These definitions can be used for teeth as well as for the whole quadrant, for example, when wanting to place a concrete element in it. The interproximal surfaces are those that contact adjacent teeth, and the occlusal surface is the one that is functional while chewing, as it contacts teeth in the opposite (upper or lower) arcade. Apical refers to the end of the root; therefore, it is the contrary to occlusal. (Figure 8). Moreover, antimer is used to refer to the symmetrical teeth in the same dental arcade. It would be the case of the central right and left incisors of the upper arcade, which are also called contralateral teeth.

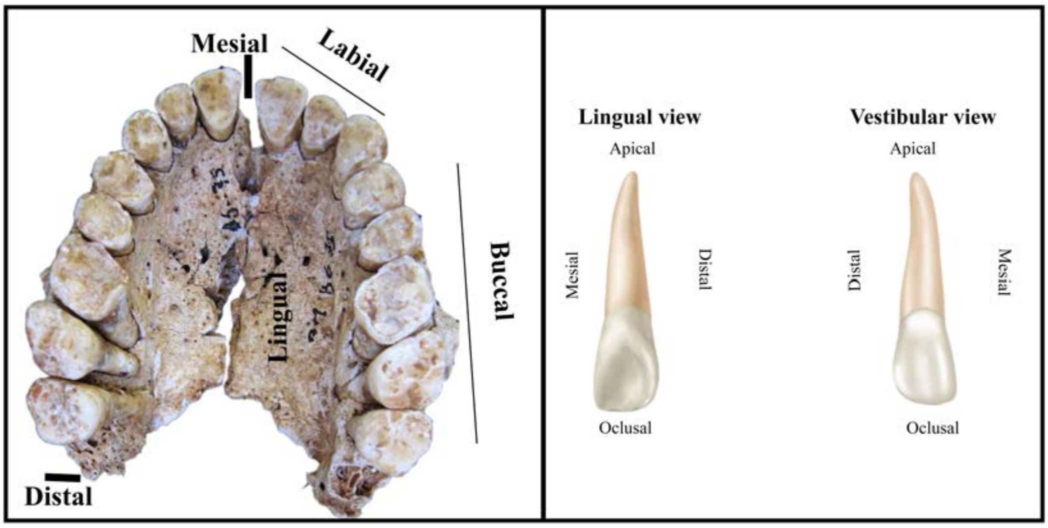

Figure 8. Details for the anatomical orientation of teeth in the maxillary (left) and the different sides of isolated teeth (right).

The potential number of cusp, their organisation and the names that are given to them varies between maxillary and mandibular molars. The maxillary ones can usually present up to five cusps, while seven principal cusps may be described in lower molars (Table 2; Figure 9).

Table 2. Number and name given to maxillary and mandibular molars, and the position of each of them in the tooth.

	Upper Molars			**Lower Molars**	
	Name	Position		Name	Position
Cusp 1	Protocone	Mesolingual	Cusp 1	Protoconid	Mesiobuccal
Cusp 2	Paracone	Mesobuccal	Cusp 2	Metaconid	Mesiolingual
Cusp 3	Metacone	Distobuccal	Cusp 3	Hypoconid	Distobuccal
Cusp 4	Hypocone	Distolingual	Cusp 4	Ectoconid	Distolingual
Cusp 5	Metaconule	Distal	Cusp 5	Hypoconulid	Distal
			Cusp 6	Entoconulid	Distal
			Cusp 7	Metaconulid	Lingual

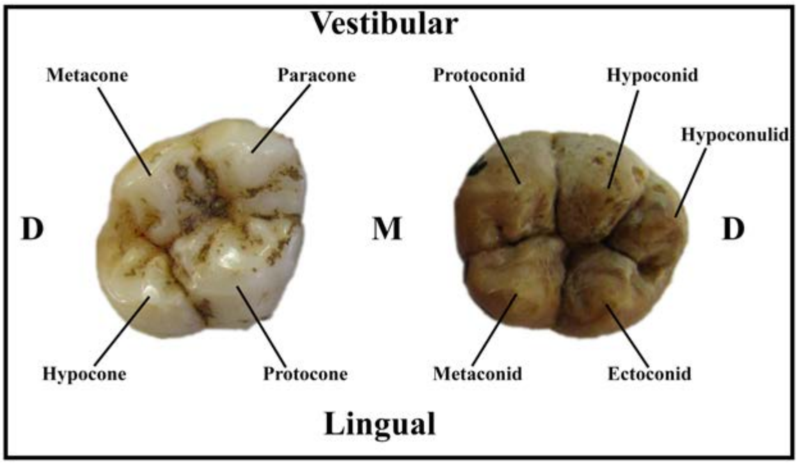

Figure 9. Pictures of maxillary and mandibular molars showing the different cusps present in each of them.

A tooth can be divided into a crown and a root (Figure 10). The crown is the part that projects into the mouth, and is the only skeletal element that directly interacts with the environment, while the root is embedded in the jaw. Lastly, crown and root meet at the cervix.

Teeth are formed by a combination of various tissues: dentine, enamel, pulp-chamber and cementum. Dentine is the core tissue of teeth; it forms both the crowns inner layer and the root. It is a hard and elastic tissue, formed from about 70% mineral elements, 18% organic material, and the other 12% is water. In the crown, dentine is coated by enamel, a protective tissue that results to be the most mineralised tissue of the human skeleton. As mentioned previously, more than 95% of enamel is composed of mineral elements (mainly crystallised hidroxiapatite), 4% organic material and 1% water. At the root, dentine is covered by cementum, a bony-like tissue that is responsible for the attachment of the cemento-alveolar joints. Cementum is formed by two kind of layers itself, a cellular layer and a non-cellular layer. Finally, the pulp chamber appears inside the dentine matrix, from the crown to the apex of the root and contains the pulp, which is the soft tissue that includes nerves and blood vessels.

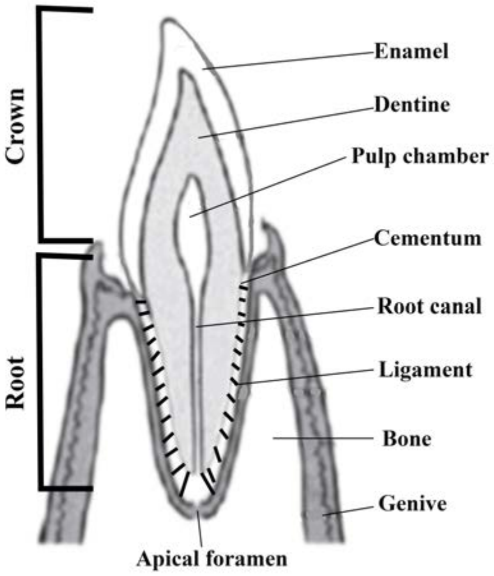

Figure 10. Representation of a cross-section of a tooth and alveole where the different tissues that from a tooth are shown (Figure created based on: Türp & Alt, 1998; White & Folkens, 2005).

1.3.2. Dental development

Taking all the anatomical details into account, it is important to understand how dental development happens in order to get an idea of how those tissues are formed and the implications it has on the final outcome (size, shape, structure of the tissues).

Although the development of dentition is a process that extends from early embryonic to adult life, most of it occurs in an individuals' first years of life. The process is divided into three main phases before eruption: initiation (tooth region and number), morphogenesis (tooth type, size, shape and cusp number) and differentiation (tooth structure: enamel and dentine formation and mineralisation). For example, at birth all deciduous teeth have started mineralization, as do the first permanent molars.

Moreover, all temporary teeth have erupted and finished root formation by the age of 3 (Figure 11). In the case of the permanent teeth, all of them except for the third molars have started to mineralise between ages 2 and 4. Third molars, on the other hand, start formation between ages 6 and 12, once most teeth have erupted. Concretely, permanent teeth erupt in 3 different moments (Figure 11): between ages 6 and 8 (incisors and 1st molar); between 10 and 12 (canines, premolars and second molar); during late adolescence and adult age (3rd molar) (Crètot, 1978; Moorrees *et al.*, 1963; Scheuer & Black, 2000, 2004).

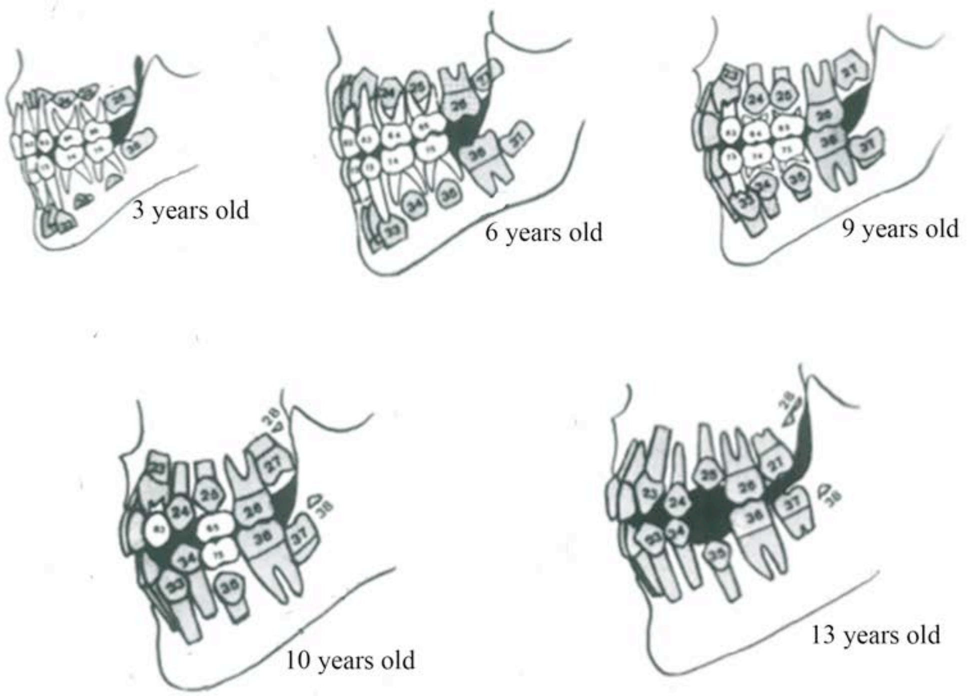

Figure 11. Dental developmental and eruption pattern from 3 to 11 years. (Figure created based on: Crètot, 1978; Moorrees et al., 1963; Scheuer & Black, 2000, 2004).

According to Scheuer and Black (2000), the time that it takes for total dental development in deciduous teeth is 2-3 years, while in permanents it varies from 6 to 12 years. Moreover, considering only the crowns it takes 4-5 years in anterior teeth and 3-4 in molars. Still, taking into account that the rest of the skeletal elements overcome growth and development through the entire life of the individual, dental development is a short process. Furthermore, once they are totally formed, teeth do not suffer any further transformation with the exception of the apposition of dental cementum and the effect of wear. This fact provides that once the teeth are functional, no environmental factor will affect the crown morphology in the way that, for example, mechanical stress modulates the shape of long bones.

All this process is regulated by the combination of genetic expression that alternates growth factors and apoptotic signals from epithelial and mesenhymal cells (Pispa & Thesleff, 2003). During tooth development, the combination of proliferation, differentiation and elimination of particular cell populations determine the final tooth shape, size and its position in the jaw. Concretely, apoptosis occurs during all the steps of tooth development: early morphogenesis, dentinogenesis, amelonegesis and eruption (Matalova et al., 2004, 2012; Peterkova et al., 2003), being the enamel knots (EK) the main structure where apoptotic cells group.

1.3.2.1. Phases, biochemical control and timing

From the previous section, we know that, dental development is divided in several phases where different aspects of tooth formation happen. Figure 12 represents a scheme of the pathways that teeth undergo in histological, genetic and signalling during development, which is explained step by step as follows.

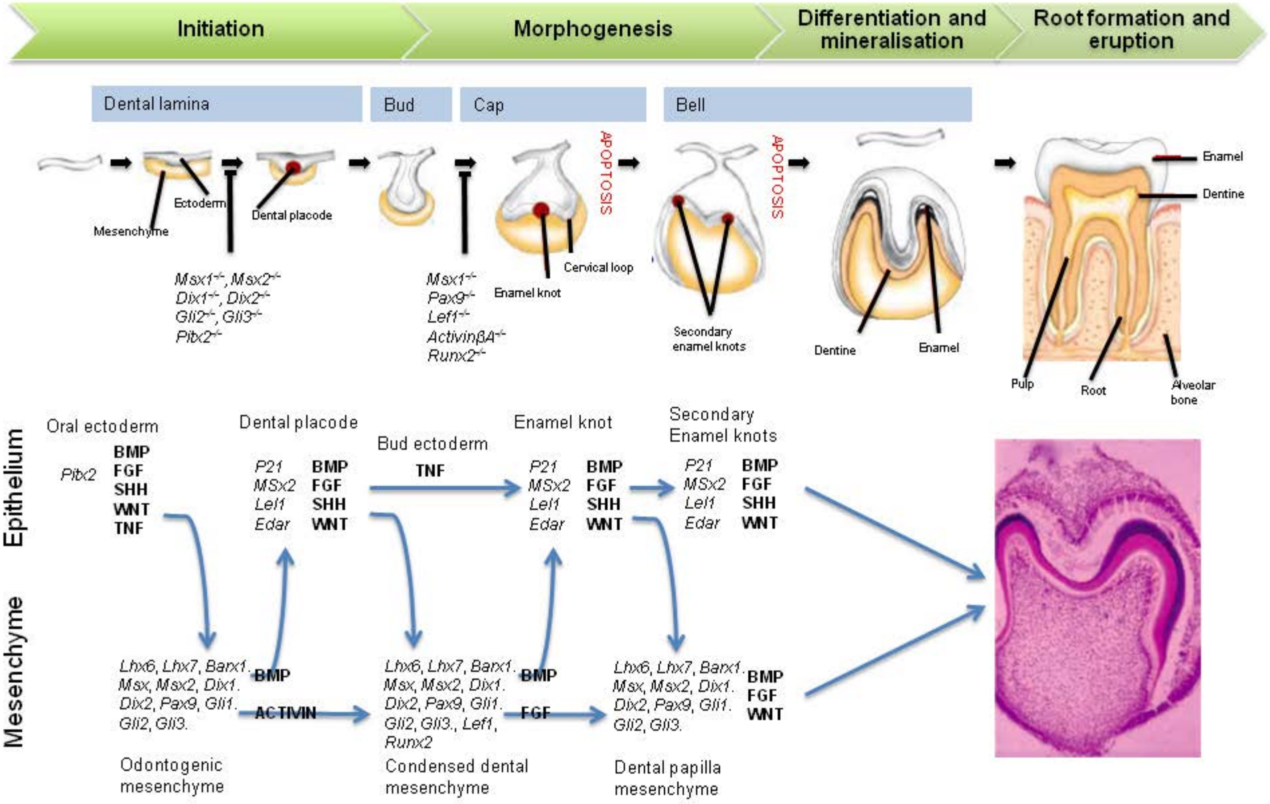

Figure 12. Phases, events occurring in the histological level (upper part), and molecular signalling (lower part) during dental development. (Figure adapted combining: Brook, 2009; Thesleff, 2003).

Initiation phase is characterised by the distinction of the dental lamina from the vestibular lamina of the epithelium. This process starts with the thickening of the oral epithelium at specific sites to form the dental placodes at about day 28 of embryonic development (Brook, 2009; Nanci, 2008; Scheuer & Black, 2000; Scheuer & Black, 2004). The formation of these placodes will determine the position where the future teeth will develop, as the bud is formed in those concrete places where the mesenchyme condenses.

The position where the dental placodes will develop is mainly determined by the interaction between mesenchymal *Pax9* and ectodermal *Fgf* and *Bmp* genes. *Fgf8* signaling from the oral ectoderm stimulates *Pax9* (gene coding for the transcription factor that induces morphogenesis) expression in the mesenchymal tissue, while in some other areas its expression is inhibited by *Bmp2* and *Bmp4* originated in the epithelium. Shortly, where *Bmp4* is present, no dental bud will be created (interdental spaces). Nevertheless, these are not the only genes involved in this stage of dental development. In fact, in *Pax9* knockout mice tooth germs develop in the same location as in wild mice. This happens due to the activity of *Pit2* and *Shh*, and thanks to the role of *Dlx* homeobox genes in early patterning of the dental field (Brook, 2009). Moreover, transcription factors in the Msx, Dlx and Lhx families are necessary to initiation and progression of odontogenesis beyond initiation. These transcription factors will regulate one another by feedback loops during this stage.

Dental germs enter **Morphogenesis** phase in a proliferating bud stage, related to both epithelial and mesenchymal cell division. This cell division makes the margins on the bud widen, giving the start point to the cap stage. The concave mesenchymal part of the cap will add to the pulp of the subsequent tooth. Meanwhile, due to histogenetic process, ten enamel organs develop from each dental lamina (Scheuer & Black, 2000). At this point, apoptotic and replacement cells group concentrically into a new structure: the primary Enamel Knot (EK). Once the primary EK disappears at the late cap stage due to the apoptosis that it has undergone, the bell stage starts. This last stage of morphogenesis is characterised by the development of the secondary Enamel Knots at the cusps in multicusped teeth.

Repeated activation and inhibition of this signalling in the EK is related to differential growth and folding patterns in both cap and bell stages, which will determine tooth dimensions and cusp patterns. Although growth stimulatory signals are expressed in the enamel knot, the cells of this same structure remain non-proliferative. The ones that proliferate and, thus, make the germ grow in size and produce the folding of the epithelium are surrounding cells and the mesenchymal dental papillae (Brook, 2009; Jernvall & Thesleff, 2000).

In the biochemical side of this process the main genes continue to be *Bmp4* and *Fgf*, with the addition of cyclin-dependent kinase inhibitor *P21*. *Pax9* induces *Msx1* expression during early morphogenesis in the mesenchyme, and both of them induce *Bmp4* expression. Together with *tenacin* and *activin* expression, cells condensate. This condensed ectomesenchymal tissue expresses *Bmp4*, *Fgf3*, *Bmp3*, *Hgf* and activin, which trigger the creation of the enamel knot (Thesleff & Nieminen, 1996). The enamel knot stimulates proliferation of the surrounding cells via *Bmp* expression. Regarding the suppression of proliferation signalling, apoptosis has been suggested as the main mechanism controlling the time-lapse of the signalling (Matalova *et al.*, 2010;). *Bmp4* actively expressed in the Mesenchymal tissue and Bmp family's members expressed in the enamel knots themselves induce *P21* expression, which leads to apoptosis (Jernvall *et al.*, 1998; Kassai *et al.*, 2005).

Once the cusp pattern has been defined with all the growth and folding of the previous phase, **differentiation** starts when the germ is at late bell stage. The cells from the cusp tips differentiate into odontoblasts (giving origin to the dentine) and ameloblasts (origin to the enamel). First odontoblasts, which develop in an apical direction, secrete the organic compounds that will form the dentine matrix, mainly collagen and other proteoglycans, glycoproteins, proteins rich in carboxyglutamic-acid, etc. Subsquently, epithelial cells differentiate into ameloblasts, which proliferate towards the occlusal surface while synthesising the elements that conform the enamel matrix, mainly amelogenin (85%), enamelin and ameloblastin. While amelogenin is essential for crystal growth, enamelin is necessary for hydroxyapatite formation in early amelogenesis.

According to Sunderland and collaborators (1987), the first deciduous incisor is the first to begin differentiation in the 15th week after fertilisation, and none of the decidual teeth enter this phase later than the 20th week of gestation. Moorreess and collaborators (1963) determined the moment in which this phase starts for several permanent teeth, and for example in both upper and lower first molars the first mineralized cusps can be observed at 3 months after birth of the individual. In the case of the second premolars and molars this would occur at about the age of 3. The last teeth to arrive to this phase are the third molars.

Pleiotrophin (Ptn) is one of the main critical growth factors for dentinogenesis, and is expressed in both odontoblasts and ameloblasts. The other main actor in the secretion of the elements that conforms both dentine matrix and enamel matrix is the *Dspp* gene (Brook, 2009; White *et al.*, 2007). This gene interacts with *Tgf-b, Bmp1* and *Mmp2* and *Mmp20* in odontoblasts during the diverse stages of dentine formation in order to control them. Moreover, *Dlx3* is also essential for dentine morphogenesis (Lezot *et al.*, 2008).

Regarding amelogenesis, *Dspp* gene also influences enamel hardness in the initial stages of the process contributing to the structural properties of the layer of enamel adjacent to the amelo-dentinal junction. *Dlx* homeobox genes are also expressed within ameloblasts during presecretory, secretory and maturation stages (Brook, 2009). According to Lezot and collaborators (2008), these genes may influence enamel formation by regulating amelogenin expression. *Runx2* is expressed in ameloblasts in order to suppress enamel protein expression and get a normal enamel thickness (Harbron *et al.*, 2009).

Following the formation of coronal dentil and the deposition of the enamel matrix, the developing tooth germs begin to form their roots. This process starts when the mesenchyme that surrounds the enamel organ and the one that is situated in the apical portion of the tooth germ proliferate. These mesenchymal cells generate both of the cells that will be part of the radicular pulp and those that will form the developing periodontium. More specifically, Hertwig's Epithelial Root Sheats (HERS), derived from cells of the cervical loop of the enamel organ, proliferate apically and control the development of the separation between pulp and periodontium. The biochemical control of this process is similar to the one directing dentine formation in the crown, and Bmp4 is one of the main regulators in HERS formation and of its activity (Thomas, 1995).

1.3.2.2. Formation of the different types of teeth

Although all the previously explained processes are common to all teeth, some control must bring a tooth germ to become an incisor or a molar. It can be clearly observed in the dentition that there is a gradient in form from incisor-like to molar-like teeth, and that some of the teeth in each group present a more variable morphology than others. Therefore, it seems obvious that contiguous teeth have influence between each other. In this scenario, two main theories tackle the mechanisms that might lead to this expression gradient: The Theory of Morphogenic Fields (Butler, 1939; Dalhberg, 1945 a); and the Clone Model (Osborn, 1978).

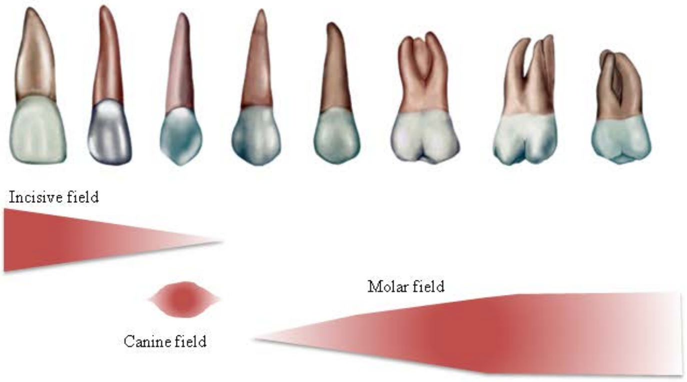

Figure 13. Scheme showing the bases of the Morphogenic Fields' theory. (Figure created based on: Ten Cate, 1998).

The first one derives from Butler's studies on the morphodifferentiation of Cenozoics mammals' teeth. It defends, therefore, that mammalian teeth are differentiated into three morphogenic fields along the mesio-distal axis of the arcades (Figure 13): incisors, canines and molars. Each of these fields would have a differential genetic influence that determines the size and shape of each tooth (Butler, 1978). At the same time, each field has influence over teeth from the contiguous one. However, the first tooth that undergoes development in the group (usually the most mesial one) is believed to have major intensity on the fields' influence. Thereby, it is considered the most stable in shape and size and referred to as 'polar tooth'. The teeth that develop later, on the other hand, can suffer more environmental influence.

On the other hand, in order to explain the development of tooth classes and the expression gradients they show, Osborn suggested the Clone Model theory (1978). This model considers that a tooth will develop in a field from a cell population (*primodium*) that will determine its configuration. Each *primodium*, will duplicate into the amount of teeth corresponding to each field (Figure 14). Therefore, the first will have all the original information from the primodium, while the rest will partially lose some information.

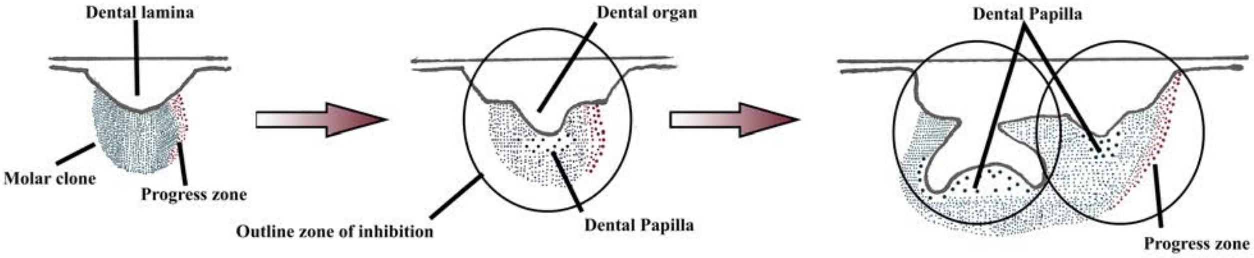

Figure 14. Scheme representing Osborn's 1978 Clone Model theory on Molar teeth. (Figure created based on: Ten Cate, 1998).

In more recent times, Sharpe (1995) developed the Odontogenic homeobox code model for dental differentiation, aiming to provide a molecular explanation for the issue. Interestingly, he suggested that dental patterns could be generated from different domains of expression of homeobox genes in neural crest derived ectomesenchyme.

More development on how an odontogenic homeobox code can produce different dental patterning was carried out by Cobourne and Mitsiadis (2006). They described how an ‘‘inter-mixing’’ of genes expressed by ectomesenchyme of the first branchial arch can lead to the establishment of different morphogenetic fields. Patterns are established by signals from the ectoderm that induce specific domains of homeobox gene expression in the ectomesenchyme. A patterning that would initially be plastic, but become fixed into the “memory” of the ectomesenchymal cells over time.

On their review of 2009, and following Mitsiadis and Smith (2006), Townsend and collaborators suggested an integrative interpretation of the three previously proposed models based on new genetic and clinical evidences. This concept is built on evidence that neural crest derived mesenchymal cells are influenced by signals from the oral epithelium in order to express homeobox containing genes (Couborne and Mitsiadis, 2006). Therefore, all three elements (the “clones” of neural crest derived cells, the homeobox containing genes in the mesenchyme, and the signalling molecules released by the oral epithelium) are believed to play important roles in patterned tooth development.

One of the most important features of this model is that it occurs in a time-dependent manner. Not only in terms of the importance of the release timing of various signalling molecules from the oral epithelium and, following the diffusion gradients that are established; but also because of the temporal expression of different combinations of homeobox genes from the proliferating neural crest derived mesenchymal cells. Moreover, it explains how nonpolar teeth are less stable due to the longer time they take in development. In this longer period that these teeth spend in their soft tissue stage, epigenetic and environmental factors may strongly influence their final size and shape.

1.3.2.3. Tooth anomalies, malformations, and their origin

This whole developmental process will have a visible outcome: the phenotype. If all the process occurs correctly, the resulting phenotype will be a “normal” one, but if due to genetic mutations (syndromic and non-syndromic), alterations on the epigenetic control of gene expression, or environmental pressure, the process will not be correctly completed, and abnormal phenotypes will be the outcome.

The line that separates between normal or anomalous variability is in some cases really narrow (agenesis of a tooth, for example); while in other cases it is clear (defects on the enamel formation, or position of the teeth). Nevertheless, it is important to take into account that many of the so-called malformations are actually extreme expressions of regular morphological traits of teeth, like elongated lower premolars (Garib & Peck, 2006).

Depending on the stage of development when the disruption occurs, the outcome will be different (Figure 15). Accordingly, when the anomalies have their origin during initiation and morphogenesis these will normally affect the number, size and shape of teeth. In contrast, when the origin is during differentiation and mineralisation phases, the phenotypes will have alterations in the histological structure of the teeth.

- *Malformations related to mistakes occurring during initiation and morphogenesis*

  The most usual anomalies that occur due to incidences during initiation are in the number of teeth, which can be either agenesis (lack of a teeth) or the presence of supernumerary teeth.

  On the other hand, when the misleading involves morphogenesis, the phenotypic outcome presents anomalies in the size, the shape and the number of cusps of teeth. These include phenotypes like macrodontia and microdontia, elongated lower premolars, the presence of extra and talon cusps.

- *Malformations related to mistakes occurring during differentiation and mineralisation*

  This group of anomalies will have an important impact in the dentine, enamel and roots. In the dentine level, three types of dentinogenesis imperfecta and two types of dentine dysplasia have been classified (Brook, 2009).

  Enamel defects are more usual and variable than those affecting the dentine. Hypoplasias, amelogenesis imperfecta, and many other phenotypes might be included in this group. Some other outcomes are consequence of both dentine and enamel dysfunction, like invaginated teeth.

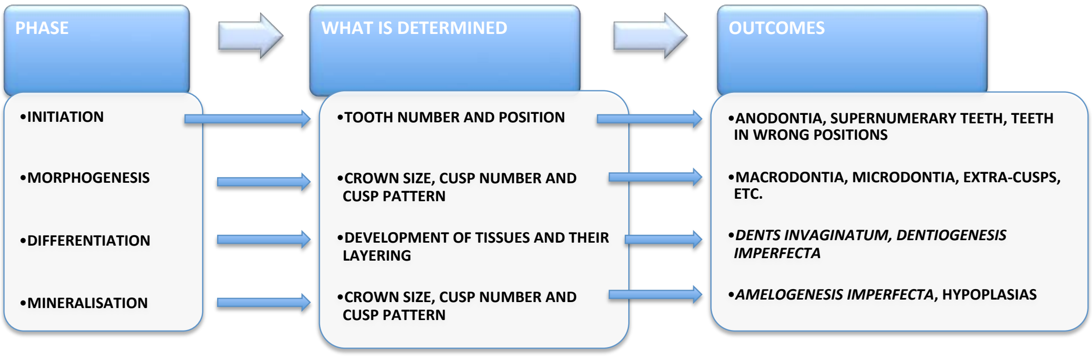

Figure 15. Scheme representing the characteristics of teeth that are determined in each phase of development, and the outcome after stress affects the individual in each phase.

These anomalies might have either genetic or environmental backgrounds. In the case of the ones originated by mutations in genes, they can also be subclasified in syndromic or not syndromic (Bailleul-Forestier *et al.*, 2008a, 2008b). When the anomaly is caused by disruption during the initiation or the morphogenesis phases, mutations in *Msx1*, *Pax9*, *Axin2*, and *Eda* genes have been found (Brook, 2009); while when they occur in the latter phases of tooth development *Dspp*, *Amelx* and *Enam* are the most usually affected genes. Finally, it has been suggested that apoptosis, which has a key role during odontogenesis, can be affected by environmental factors that downregulate Bmp production (or Bmp-induced molecules) via epigenetic control (Riga *et al.*, 2013).

Teeth recovered from archaeological contexts are not alien to anomalies either, as numerous dental anomalies have been described too: supernumerary tooth (Broehm *et al.*, 2011; Duncan, 2009; Mays, 2005), tooth fusion (Benazzi *et al.*, 2010; Padgett 2010) and accessory cusps, such as talon cusps (Mays, 2005, Stojanowski & Johnson, 2011).

1.3.3. Dental Anthropology

Dental Anthropology, according to the *Medical Dictionary for the Dental Professions,* or as defined by Hillson (1996), is “A branch of physical anthropology concerned with the origin, evolution and development of the dentitions of primates, especially humans, and to the relationship between primates” dentition and their physical, social and cultural relationship”.

Taking into account the characteristics mentioned before, and that the pathologies affecting dental tissues are higly informative on diet, adaptation of the groups to different environmental conditions, indicative of concrete physiological stresses suffered by the individuals and cultural activities practiced by the groups, studies in dental anthropology are useful in order to obtain information about human populations.

It seems obvious that these characteristics that are applicable to modern day humans, might also be useful for reconstructing similar information in archaeological remains. This is important, as mentioned before, because their great resistance makes teeth the best-preserved remains in archaeological contexts, in many cases the only ones that might be analysed.

For example, the presence of cavities inform about diet and sugar consumption (Hillson, 2001; Liebe-Harkort, 2012); the presence of calculus is highly correlated to a high protein consumption in diet (White, 1997), while the analysis of the phytolites, starch and fibres accumulated keep direct record of food consumption, environment, and activities (Hardy *et al.*, 2009; Hardy *et al.*, 2012); dental wear informs about the hardness of the diet (Ungar, 2004), might be used as an age-at-death indicator, and also used to study masticatory and non-masticatory use of teeth (d'Incau *et al.*, 2012; Lozano *et al.*, 2008, 2009), as well as it can inform of direct cultural modifications (Scott & Turner, 1997). Moreover, both calculus and enamel hypoplasias can be affected by and, and therefore, reflect concrete environmental stressors (Lieverse *et al.*, 2007; Subirà *et al.*, 2016). Metric traits have been a basic tool for studying intra and inter population variation, evolutionary patterns and sexual dimorphism in human groups (Calcagno, 1989; Frayer, 1978). Furthermore, the most accurate method for calculating the age-at-death in adult skeletal remains is the study of the formation of cementum layers (Lanteri, 2016).

1.3.3.1. History of studies in dental anthropology with focus on ancient skeletal remains

Although the concept dental anthropology did not show up until the XX century, human dentition has been studied for several centuries in descriptive modes. Eventually, this discipline derived mainly from odontology and dentistry, the classical scientific discipline dealing with fundamental questions about the development and structure of teeth (Alt *et al.*, 1998 a; Peyer, 1968).

From this aspect, researchers have worked in the study of dentitions since the antique Greece. For example, Hippocrates' *Corpus* represents one of the oldest written documents that addressed teeth, and Aristotle's *De generatione animalium* represents one of the first records that include comparative anatomical observations about teeth. Also, the most remarkable source of general anatomical knowledge, and dental anatomical knowledge too, is Galen's *De anatomicis* *administrationibus*, which was used and compiled by several authors and kept alive until the end of the Middle Ages.

In the XVIII and early XIX centuries scientific approaches led to improvements in several areas, including the research on dentistry. This is reflected in the studies about origin, development, morphology, and structure of teeth (Alt *et al.*, 1998a). Important contributions were made to basic dental knowledge during the XIX century. Anatomists, histologists, and dentists made important contributions to basic dental knowledge during the XIX century; and they mainly focused on the histology of structural elements of teeth (Alt *et al.*, 1998 b). These studies also contributed to the initiation of investigations in comparative anatomy and zoology.

In this field Owen (1840-1845) published “Odontography”, the first comprehensive monograph on the comparative dental anatomy of living and fossil animals (Alt *et al.*, 1998 b). All this work affected positively on early research of teeth phylogeny. This modality, thought, was primarily oriented towards comparative anatomy and systematics, due to the influence of the founder of palaeontology, G. Cuvier.

During this century the interest in studying of ancient skeletal remains from the perspective of teeth increased drastically. One of the main reasons to impulse this research was the high rates of caries found in modern British population, and the aim to find an explanation to those rates (Mummery, 1870) by comparison to those found in archaeological samples. Therefore, after an extensive study of skeletons from different periods of the British Island, Mummery determined that primitive groups presented lower rates of decay compared to more civilised groups. He argued that this relationship was based on an inferior quality of teeth structure in the latter due to a poorer diet. This theory of “weaker teeth” would survive for a long time as will be further explained.

Miller (1883) suggested that caries is produced by the acids synthesised in the fermentation of carbohydrates and their interaction with imperfections in the structures of teeth. It was few years later (1913) when Turner and Bennett demonstrated that caries are related to sugar and starch fermentation by microorganisms.

In relation to these studies in dental caries, some more were made regarding wear and histology and enamel defects. Mummery (1870) observed differences in the wear patterns related to the sand and grit that was included into food during its processing. He also made some observations on the direction of the wear facets, and he noticed that oblique wear was related to chewing though and hard food. Nevertheless, all his observations were merely qualitative and no scoring standard was developed until 1879, when Broca developed his method. Hrdlička (1908, 1909) would use Broca's method in order to describe dental wear in several collections. Nevertheless, he saw the possibility of using this indicator as an age-at-death determination method for skeletal samples, which he would publish later on (1920). In his 1908 and 1909 works he also described the high frequencies of shovel shape incisors in Native-American groups. And, although it was recognized as a significant distinguishing characteristic among this group, no further advances came in dental morphology due to the popularity of cranial morphology studies (Rose & Burke, 2006).

Regarding the histological studies and the defects on the structure of teeth, Mummery (1870) suggested that disease; minerals in food or medicine could have effects in dental development, leading to defects on the structure. As recovered by Rose and Burke (2006) Berten and Black described physiological disturbances reflected in dental microstructures and compared enamel's surface and histological defects with local and systemic disturbances; in 1895 and 1900 respectively. Moreover, Tomes (1892) also determined that it was possible to study ancient teeth histologically by means of microscopic analysis. Therefore, he put the first milestone in the study of microstructure and taphonomy in archaeological teeth.

It is also important to mention that, during this period and afterwards, most of the advances in dental anthropology applied to ancient skeletal remains have been issued to determine the presence of agriculture and its development, which has been one of the main archaeological questions of the XIX and XX centuries.

The period between the two World Wars was a period of settling-in in dental anthropology: a period of development of chronology and reinforcement of existing knowledge. This included further studies in archaeological collections based on the possibilities of understanding ancient populations provided by previous studies. It was also a period of gathering combined dental and ethnographic information in order to understand dental evidences and being able to develop inferences based on them. In this sense, data from many parts of the world were soon available, including Africa, Australia and the Arctic (Buxton, 1920; Campbell, 1925; Nicholls, 1914; Oranje et al., 1935; Orr & Gilkes, 1931; Schwartz, 1946; Staz, 1938; Waugh, 1928, 1931, 1933). Campbell (1925) made some observations in Australian aboriginals that related some features in environment and diet to the great amount of wear and low incidence of diseased teeth observed. On the other hand, differences flourished relating less dental wear in African pastoralists (who had soft diets) in comparison to agricultural neighbours (Buxton, 1920).

The study of four different prehistoric Native American groups with different subsistence patterns demonstrated that agriculturalists present more decay than hunter-gatherers (Leigh, 1925), in the first significant application of clinical and ethnographic knowledge in skeletal dental anthropology. Also, it was suggested that there is a relationship between maize agriculture and consumption and decay (Colquitt & Web, 1940). Moreover, it was also concluded that the Sioux group had less wear than others because of the lack of use of stone grinders to prepare the maize consumptions.

Nevertheless, still in 1930, Hooton related the 47.9% prevalence of caries in Pecos Indians to a poor diet that resulted in imperfect dental structure. In any case, further studies clearly showed the link between high sugary diets and an increase in decay (Rose & Burke, 2006).

Although Buxton's (1920), Campbell's (1925) and Leigh's (1925) studies supported a correlation between physical consistency of diet and rates of dental wear, the study of the same in skeletal remains focused on age at death determination.

Hrdlička (1920, 1921) followed up with his work on recording morphological variations on teeth and increased the amount of traits that he observed. He published solid standards for recording shovel-shape incisors, which would help other authors to do so, but he did not develop the standards for the other traits. In any case, due to the lack of standardization and, probably, due to the impact of the statement that little morphological differences were to be found among races by Gregory (1922), studies in dental morphology did not blossom in anatomically modern human remains. Nevertheless, a push was observed in the study of the same kind of characteristics in fossil teeth. The measurements of teeth were also standardized, and applied in fossil remains (Rose and Burke, 2006). Campbell (1925) did also record metrics in Native Australians, but still it did not become a main resource in anthropological studies, because the main means of establishing racial affiliation and reconstructing migration of ancient populations was by cranial types (Hooton, 1930).

Considerable progresses weremade in the following years on research focusing in dental structure, odontogenesis, anomalies and defects. Among this subject various works were realized about the relationship between physiological growth disturbances, dental defects, and caries. But most importantly, there were studies regarding the relation between time of tooth development and histological structures (Rose & Burke, 2006), and the relationship between various diseases and disturbances with dental defects. Therefore, the origin of hypoplasias and themselves were studied and described. Moreover, Sognnaes (1955) analysed sections of 233 archaeological teeth and described that they were not superior in structure although they presented less degree of disease.

Many new aging methods through dental wear continued being developed between 1939 and 1950 (Hrdlička, 1939; Zuhrt, 1955; Murphy, 1959 a; 1959 b). Although it was clear that diet affected wear patterns and this was a factor taken into account for these new methods, few wear studies were carried out with the aim of reconstructing diets after Leigh (1925). As for dental morphology, the 1950s were a period of basic research to establishing the genetic foundations of morphological variations (Scott & Turner, 1997). Furthermore, Dahlberg (1951) published his study on the Pima dentition, establishing standards for recording morphological variation on teeth, and created plaques that would be distributed the following years. It was after 1963 (a), year in which Brothwell published his book *Dental Anthropology* that the studies of teeth in human skeletal remains definitively became important and up to date with clinical knowledge. This publication influenced all the areas concerning the research done in previous years. Moreover, it came along with a push in technological improvements, such as the automatization of electronic microscopes, measuring devices, and all the scanning techniques that are still developing nowadays. Cohen and Armelagos' (1984) book in palaeopathology also helped in the application of dental studies in order to determine the origins of agriculture.

Caries were definitely used in order to make dietary inferences from dental pathology, but there was no threshold in order to determine if a population was agriculturalist or not. Turner took on the task of determining it, and in his study of the Jomon from Japan (1979); he determined that hunter-gatherers would not exceed a 1-2% of prevalence of caries.

Brothwell (1963 b) developed a simple diagram of dentine exposure in order to determine age-at-death of the skeletal remains, and Smith (1972) and Lunt (1972) developed new methods. But at the same time some researchers started to use wear analyses for dietary reconstruction, mainly in two ways: by analysing the wear angles (something Mummery (1870) had already suggested), and developed by Hinton (1981), Molnar (1971), and Smith (1984); and by the analysis of microwear using microscopes. This later method was first intended by Dahlberg and Kinsey (1963) using a light microscope, and developed further by Walker and collaborators (1978) with the adoption of the electronic microscope (SEM). This was really useful for fossil diet reconstruction, but it was not extensively used, due to the economic expense and time requirement, until the semioautomated systems were developed. Nevertheless, it is one of the main ways to determine fossil diet currently (Ungar, 2004), and it is also used to study non-masticatory uses of teeth too (Lozano et al., 2008; 2009).

Swärdsted conducted the first systematic study of hypoplasias (1966), and determined that those were more frequent among lower social class individuals. This put some basics on the following studies in order to determine stress in childhood and during development. In the same sense, although dental measurements have mainly been used to compare populations (Frayer, 1978; Calcagno, 1989), they have also been used to study fluctuating asymmetry as a marker of stress in skeletal populations (Barret, 2005; Barret *et al.*, 2012).

Finally, Brothwell's book also helped promoting dental morphology as a tool to assess population affiliations and to document migrations among ancient peoples in the chapter by Dahlberg (1963). As it will be explained in further detail, in later periods, and with the development of complete scoring systems (Turner et al., 1991), dental morphology would become a main subject of study in the research of the origin of ancient populations (Coppa *et al.*, 2007; Cucina *et al.*, 1999; Irish, 2006; Scott & Turner, 1997).

1.3.4. Dental Morphology

The study of dental morphology is based on the analysis of the phenotypic characteristics of teeth. The considered discrete traits are those such as cusps, tubercles, grooves and ridges from the crown and roots of teeth (Scott & Turner, 1997). These characteristics are supposed to be selectively neutral (Manabe *et al.*, 2003), and thus chance, and not functional selection, influences the presence of a concrete trait, or traits in a population. Moreover, in the same way, due to the lack of selective pressure, it is more likely that in the absence of major demographic events their proportions would be maintained (Ember *et al.*, 2006).

In another sense, taking into account the strict genetic control that rules odontogenesis (Brook, 2009; Cobourne and Mitsiadis, 2006; Sharpe, 1995; Townsend *et al.*, 2009 a), it is just logical to see dental morphology as a highly genotype-representing phenotypic expression compared to the phenotype of other anatomical structures. Many studies have addressed the issue of the genetic origin and heritability of these dental non-metric traits. Dental development is strongly determined by gens and, thus, dental morphology patterns as well. Those traits are inheritable, because they are the phenotypic expression of several inheritable genetic characters.

According to Scott & Turner (1997) the control of most traits has a multigenic origin. Nevertheless, according to Graber and collaborators (2006) some dental traits would be controlled by just one kind of gene; in the same line, Scott and Turner (1997) also suggested that some traits are mainly regulated by just a gene.

Therefore, these analyses became an interesting source of information to establish the biological relationship level and affinities between human groups, migration and adaptation-patterns and, in the same time, that allow determining the ethnic and geographic origins of different human populations. Moreover, it has been reported that biological distance matrixes obtained studying dental morphology correspond to those obtained analysing nuclear DNA (Hubbard *et al.*, 2015).

1.3.4.1. Dental non-metric traits

When we talk about dental non-metric traits, we consider all the anatomic variations observed over the dentition. Usually, those characters can be either present or absent, and many times they can be present in different levels of expression (Figure 16). As mentioned previously, they can be positive structures such as accessory cusps, tubercles or crests; or negatives like grooves. But some other characteristics like the variation on the number, position, and size of both cusps and roots are also considered non-metric traits.

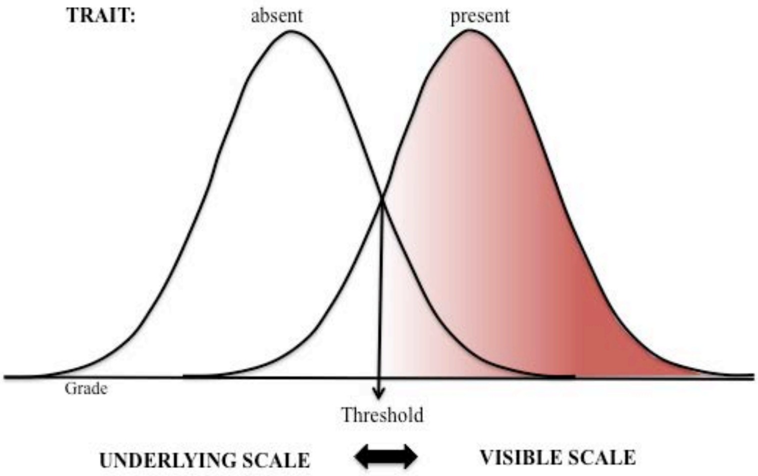

Figure 16. Representation of the quasicontinuous variation and threshold effect in non-metric dental traits. The two overlapping normal distribution curves illustrate the continuous basis of the traits. The threshold point separates the visible and the underlying scale. The individuals with genotipes to the right from the threshold point will present visible phenotypes in different grades of expression (gradient), while those with genotypes to the left will not manifest the trait (absence). (Figure created based on: Scott & Turner, 1997).

Therefore, focusing on the way the traits can appear we can divide those traits into three main groups:

1. Dichotomic traits: these are the traits that can be classified as present or absent.

2. Graduated and ordered traits: these characters are observed in relation to their developmental state. They can be absent or present, but show different expression levels.

3. Traits with not ordered but variable expression: This last group is the one that includes traits such as the *winging of incisors*, the *interruption groove* or *groove pattern* of the mandibular molars. They are all characterised because there can be more than three forms, but they are not different developmental states of a trait.

Some of the traits are observed both in the decidual and permanent dentition. Nevertheless, due to the lower frequency of children burials and the lesser preservation of the remains, most studies in dental morphology focus on the permanent dentition (Desideri, 2007; Scott & Turner, 1997). Moreover, although more than 100 traits have been reported in the human dentition, not many of them (around 30 or 40) have been well defined, standardized, and subjected to detailed anthropological analysis (Figure 17). In this sense, the scoring method that comprises more traits and is used worldwide is the one developed by Arizona State University (ASUDAS) (Turner *et al., 1991*).

This method describes and illustrates 35 dental traits (Table 3) that, when applied to a full dentition, provides the researcher with 121 variables. The fact that it is the most used scoring method has the advantage that comparative data from many populations are available in the literature.

Finally, it is important to keep in mind that not all variables will be informative for the question asked by the researcher, because for example, there can be traits that are absent in all the analysed samples. Therefore, it is important to thoroughly select the most adequate traits.

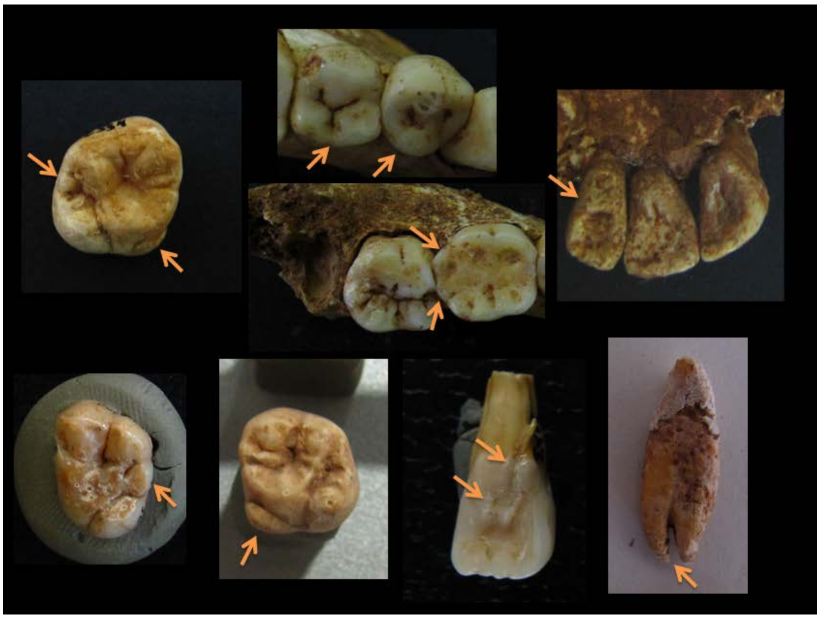

Figure 17. Examples of different traits scored in the work. Upper Row (all the pictures belong to remains recovered from Bòbila Madurell site, left to right): first right molar showing small 5th cusp and small Carabelli's Tubercle; P_3 with a single lingual cusp and P_4 with two lingual cusps; 6 cusped lower first left molar (arrows signal cusps 5 and 6); upper second incisor that presents severe shovelling. Lower Row (left to right): second superior left molar with a big 5th cusp (Can Sadurní, Capa 9); first superior left molar with large expression of Carabelli's Tubercle (Pico Ramos); first superior right incisor that presents marked Tuberculum dentale and Interruption Groove traits (Iruaxpe I); two-rooted lower right canine (Collet Redon).

Although genes on the sex chromosomes play a role in dental development, little or no sex dimorphism is usually observed on the phenotypic level regarding crown and root traits, with few exceptions. Moreover, when differences are found, they are usually inconsistent among samples and are low-order in magnitude (Scott & Turner, 1997). In most cases it is Carabelli’s tubercle (Goose

& Lee, 1971; Kaul & Prakash, 1981; Kieser & Preston, 1981; Townsend & Brown, 1981; Scott *et al.*, 1983), shovel-shaped incisors (Harris, 1980), or Distal Accessory Ridge of the upper and lower canines (Kaul & Prakash, 1981; Kieser & Preston, 1981; Scott, 1977; Scott *et al.*, 1983) that have shown any differences. Therefore, dental morphological traits present an advantage, which they share with autosomal genetic traits, that male and female data can be pooled to estimate population frequencies. This feature is of special interest in small skeletal collections, because it allows using the sample as a single unit, in contrast to metrical analyses that require splitting it by sexes.

Some of the traits are more discriminatory than others regarding major population groups (African Population, Asian Population, Native-American Population, Aboriginal Australian Population, or Caucasian Population). This is the case of the Shovel-shaped incisors, Carabelli's tubercle, or the 7th cusp in mandibular molars (Scott & Turner, 1988; Heather, 2005). As it is well known, Asiatic and Native-American populations present higher frequencies of Shovel-shaped incisors; Caucasian and African populations in contrast are characterized for a high presence of Carabelli's cusps; and the 7th cusp is typically found in sub-Saharan African samples.

In fact, based on the characterisation of worldwide populations and the study of the frequencies of many crown and root traits in each of them, Scott and Turner (1988, 1997) present some overall classification of major modern human groups. In this classification they distinguish Western Eurasians, Sub-Saharan Africans, Sino-Americans, Sunda-Pacifics and Sahul-Pacifics. Although it is not a closed classification, it might help, to some extent, in forensic cases or archaeological samples to build a first approach idea in order to rule out possible origins of the individuals. In most recent times the Eurodont dental complex has been described in order to diferenciate Western Europeans from the Caucasic group (Scott *et al.*, 2013).

Table 3. List of the traits described and standardysed in the ASUDAS methodology (Turner *et al.*, 1991).

Trait	Deffinition	Teeth where it is appliable
Incisive Winging	Rotation of superior central incisives.	UI1
Incisive Curvature	Degree of convexity of superior central incisives' labial surfice seen from occlusal view.	UI1
Shoveling	Presence of marginal elevations in the margins of the lingual side of the teeth.	UI1; UI2; LI1 LI2
Double-Shoveling	Presence of marginal elevations in the labial side of teeth.	UI1; UI2; UC; UP3; LI1; LI2
Interruption groove	A groove that crossess the cingulum and sometimes sections the root.	UI1; UI2
Tuberculum Dentale	Tuberculum situated in cingulum area of the lingual face.	UI1; UI2; UC
Peg-shaped incisor	Size-reduced incisors.	UI2
Canine Mesial Ridge	Expression of the mesiolingual and distolingual elevations on the canines.	UC
Canine Distal Accesory Ridge	Elevation observed at the distolingual fossa, between the apex and the distolingual elevation.	UC; LC
Premolar mesial and distal accessory cusps	Presence of cusps at the mesial or distal extremes of the sagital groove.	UP3; UP4
Tricuspedpremolar	Presence of a third cusp of the same size in upper premolars.	UP3; UP4
Distosagittal ridge	Elevation that appears from the bucal cusp's apex to the distal extreme of the occlusal side.	UP3
Odontome	Pin-sized enamel projections in the oclusal surfice of premolars.	UP3; UP4; LP3; LP4
Enamel extension	Apical projections of enamel in the cingulum area.	UP3; UP4; UM1; UM2; UM3; LP3; LP4; LM1; LM2; LM3
Metacone	Size of cusp 3 in maxillary molars.	UM1; UM2; UM3
Hypocone	Size of cusp 4 in maxillary molars.	UM1; UM2; UM3
Cusp 5	Presence and degree ofthe metaconule in maxillary molars.	UM1; UM2; UM3
Carabelli's trait	Presence of a tubercle in the lingual surface of cusp 1 of maxillary molars.	UM1; UM2; UM3
Parastyle	One of Bolk's paramolar cusp. Presence of a cusp in the buccal surfice of cusp 2 or 3.	UM1; UM2; UM3
Peg-shaped molar	Size-reduced molar.	UM3
Root Number	Number of roots present in teeth. In order to consider different roots, those must be separated at least between a quarter and a third of the whole root lenght.	All teeth
Radical Number		All teeth
Congenital Absence		UI2; UM3; LI1; LM3
Premolar lingual cusp variation		LP3; LP4
Tome's root	Deep mesial channel in the root.	LP3
LM1 Anterior Fovea	Presence of a mesial groove and elevation.	LM1
Groove Pattern		LM1; LM2; LM3
Cusp Number		LM1; LM2; LM3
Deflecting wrinkle	Shape of the medial crest of cusp 2.	LM1; LM2; LM3
Distal Trigonid Crest	Crest or loph that conects cusp 1 and 2.	LM1; LM2; LM3
Protostylid	Paramolar cusp in the buccal side of cusp 1.	LM1; LM2; LM3
Cusp 5	Presence of the Hypoconulid.	LM1; LM2; LM3
Cusp 6	Presence of the Entoconulid.	LM1; LM2; LM3
Cusp 7	Presence of the Metaconulid.	LM1; LM2; LM3
Torsomolar angle	Degree of rotation of lower third molars.	LM3

1.3.4.2. History of the studies on dental morphology

Dental morphology is not a new knowledge area in Anthropology, as some of these traits were described long ago, such as supernumerary teeth, Carabelli's cusp, shovel-shaped incisors and the presence of several tubercles.

As mentioned by García-Sivolí (2009), althought the interest for these traits started in Ancient Ages, human dental morphology studies started during the XIX century, principally with the works by Cuvier, Lyell, Owen, Huxley, and Darwin. Indeed, it was in 1842 that Georg von Carabelli described the accessory mesiolingual cusp in the upper molars that is common in European dentitions. Later, more characteristics of dentition were described by several authors: supernumerary teeth, congenital absence of the third molar and peg shaped ones, winging of upper incisors, shovel shaped incisors, among others.

Along the XX century the studies on dental morphology started to become important for physical anthropology, although it was not without a great effort (Scott & Turner, 1997). In this sense, Hrdlička wrote in 1920 the first paper that would classify expression degrees of a morphological trait, the shovel-shaped incisors. He had by this time the advantage of studying skeletal collections in the US National Museum of Natural History and could base his work on that of previous researchers, so he assessed this variation in several human groups and also described its occurrence in nonhuman species. The main finding on this work was the similarity between Amerindian and Asian samples, and the well-defined difference of those from Europeans and Africans. This paper was followed by a new one that extended the studies to several characters (Hrdlička, 1921).

Further works took place in the following years influenced by Hrdlička's, of which the most transcendent are the following: *The Origin and Evolution of Human Dentition* by W.K. Gregory (1922), *Dentition and Palate of the Australian Aboriginal* by T.D. Campbell (1925) and *The Teeth, the Bony Palate and the Mandible in Bantu races of South Africa* by J.C.M Shaw (1931).

Despite the insistence of these authors on the importance of the study of dental morphology and comparative studies based on it, as well as the discriminatory results they were obtaining, anthropologists showed no major interest until the 1940's. After the 1950s, important contributions were made to studies on genetics and morphogenesis of tooth crown traits, and aspects such as the forensic potential of dental morphology were reviewed (Scott & Turner, 1997).

A.A. Dalhberg and P.O. Pedersen where the main promoters of comparative and intensive studies on dental morphological variation (Scot & Turner, 1997). Thanks to their work, dental morphology in American Indians and Greenlandic Eskimos was described (Dalhberg, 1945 b, 1951; Pedersen 1949). They were the promoters of more active international communication among researchers focused on human teeth as they organized the first International Symposium on Dental Morphology in 1965. Moreover, Dalhberg made the first attempt of standardising the observation of morphological traits by the release of a series of reference plaques for several traits.

It is noteworthy the work of the Japanese researchers, who had an active program of dental anthropology during the XXth century. Due to language barriers though, the diffusion of their research with occidental scholars was difficult. Nevertheless, after the 1950s this changed with the leadership of K. Hanihara, who based on the work of previous researchers developed a strong tradition of dental morphological studies among Japanese anthropologists, and published in international journals, meetings and books, as well as in Japanese ones (Hanihara, 1963; Hanihara 1968).

Nevertheless, for many decades, studies were carried out without using a standardized methodology. In order to standardize the studies Turner and colleagues developed the *Arizona State University Dental Anthropology System* (ASUDAS) methodology in 1991. This system recovered a sample of comparative studies carried out during almost a century (García-Sívoli, 2009) and established some standards that allow an easy replication of the observations. These consist basically on graduation of the expression shown by the traits and the recompilation of sample plaques showing the levels following Dahlberg's work (1956). Moreover, these plaques can be distributed between researchers with the aim of standardizing the scored values. The characters described in this methodology present no sexual dimorphism or variation during the time.

1.3.4.3. Genetic basics of trait inheritance

Even though many researchers have tried to identify single genes responsible of the expression of each trait, the studies have not been successful. Nevertheless, trait inheritance neither follows Morton's and MacLean's complex segregation model (1974) as shown by Kolakowski and collaborators (1980) and Nichol (1989). Their results indicated that even though the inheritance model was not as simple as a Mendelian one, it is not as complex as classical multigenic ones.

Moreover, they identified that most of the variation should be accounted to one gene, but this one interacts with many others (Scott & Turner, 1997).

As stated previously, most dental nonmetric traits are not just present or absent, but there is a wider expression scale for them. Therefore, they are defined as quasicontinuous variables, a concept described by Grüneberg (1952) in order to refer to non-continuous phenotypes that would not follow a Mendelian mode of transmition, but a polygenic one. This concept was included in anthropology by Berry and Berry (1967) and Berry (1976). Therefore, with this name, these traits are differentiated from discontinuous traits, which present a simple inheritance model; and continuous traits, with complex inheritance mechanisms (Grüneberg, 1952).

The model suggested for the expression of quasicontinuous variation is the one based on 'threshold dichotomies' developed by Falconer (1965) and mentioned by Wright (1968) to distinguish such traits from 'point dichotomies' that do have simple modes of inheritance. This model is understood in two scales that overlap each other, like two normal distribution curves with one threshold (Figure 16). Therefore, it can be divided into an underlying scale (determined by both genetic and environmental factors) and a visible scale (phenotypic values directly observable). Moreover, the threshold zone will take part of each of both scales. A distinctive feature of this two-scaled model is that the visible scale is discontinuous, while the underlying one is continuous (Scott & Turner, 1997). Accordingly, a trait will be expressed when the underlying scale (mainly genotype depending) arrives to the threshold. All of this means that genotypically different individuals can be identical in phenotypic values, because, for instance, even if one is close to the threshold value of the underlying scale both will not express the trait.

As pointed out by Grünenberg (1952) there are some qualities that distinguish quasicontinuous variants from characters with simple modes of inheritance. The main ones are the following: 1) a continuous distribution may occupy any position relative to a physiological threshold; 2) that there is a positive correlation between trait incidence and expressivity, so that populations with higher frequencies of a trait should present more individuals with pronounced trait expression too; 3) the multiple genes responsible for the expression of these variables are additive and sensitive to environmental effects.

Based on animal models and the observation of variable expresion showed by nonmetric crown traits, Sofaer (1970) was among the first dental researchers that defended the quasicontinuous nature of nometric tooth crown traits. Consequently, many researchers have made efforts to determine whether or not these traits follow the characteristics described by Grüneberg. The most important of these studies are Scott's (1973) and Harris' (1977). The former studied segregation patterns of 20 crown traits in American white families, while the second analysed 11 traits in 21 teeth in 315 Solomon Island families.

Scott (1973) found that many of the patterns approximated the expectations of autosomal dominant or recessive inheritance, but that there were a few offspring that violated the laws of simple autosomal inheritance. Therefore, the whole spectrum of the results could not be explained by simple Mendelian inheritance, but could be predicted by the threshold model. On the other hand, while the correlation between incidence and expressivity was maintained for shoveling, Carabelli's trait did not show significant correlationship. Harris' (1977) study concluded that tooth traits were quasicontinuous variants with polygenic modes of inheritance, but that not all traits were necessarily inherited in the same manner. This was because he found that high frequency traits simulated the ratios expected for Mendelian dominance while low frequency traits simulated recessive inheritance ratios. In summary, both authors concluded that the studied traits were quasicontinuoum traits, but that action of major genes, modifier genes, dominance and epistasis influencing the expression of other traits cannot be excluded from the mechanisms of inheritance and variable expression.

Following these discoveries, Kolakowski's and colleage's (1980) work and Nichol's (1989) work on the analysis of complex segregation for the traits found that probably a few genes and loci are involved in crown trait development. They also found that there are some traits that have greater influence of a single gene than others. Those genes with the influence of a major gene would be: Carabelli's trait in the families of Salomon islands (Kolakowski *et al.*, 1980); and 12 traits on Nichol's study on Pima Indians (Nichol, 1989). Nine of these traits - UI2 shoveling, incisor and canine double-shoveling, Carabelli's trait of UM1, multiple lingual cusp of the lower premolars, the hypoconulid of LM1 and LM2, cusp 7, and the maxillary torus - show signs that the allele for affection by the trait is dominant; while 3 of them - hypocone of UM1 and UM2, transverse ridge of lower premolars, and the maxillary torus - show evidences of a recessive allele for expression of the variation.

No genes responsible for a "normal variable" trait have been found yet, but a recent paper by Kimura and colleagues (2015) reported significant correlations between a polimorfism of *WNT10A* gene and the expression of some dental non metric traits (UI1 shoveling, LP4 distolingual cusp, UM1 cusp5, and LM2 Hypoconulid). In addition, researchers have linked malformations and weird or extreme variations of some traits to concrete alleles and mutations in families or small regional groups (Desideri, 2007; McKusick, 1990), and more than 60 dental anomalies are categorised in the On-line Mendelian Inheritance in Man (OMIM). In these cases, tooth agenesis is one of the most studied traits, and it is used as a non-metric trait in the analysis of biological affinities between and within populations. For example, Vastardis (2000) found that there was a mutation in the *MSX1* gene of all members of a family showing agenesis of second premolars and third molars; and a more modern study by Rodrigues Paixao-Côrtes and collaborators (2011) also showed relationships between mutations in *MSX1* and *PAX9* genes and agenesis of different teeth. Both genes, as mentioned before are key factors in different moments of dental development.

Taking into account that environmental factors can epigenetically affect dental development (Riga *et al.*, 2013), different studies have been carried out in order to assess the potential effects that this might have on the discrete variables of teeth. Some of the studies, which analysed the intake of fluoride (Cox *et al.*, 1961; Møller 1967), different conditions on the mother (diabetes, hypertension and hyperthyroidism) (Garn *et al.*, 1980) or secular changes (Ebeling *et al.*, 1973) show changes on the size of the teeth and cusps, but not in the morphology. Studies analysing populations migrating to environmentally different zones and their descendants show neither differences on the morphological outcome of teeth in contrast to some cranial variations that do change (Hallfman *et al.*, 1992; Lasker, 1945; Scott & Alexandersen, 1992; Scott & Turner, 1997).

Twin studies have been used for long time in order to determine how strong the inheritance pattern of a trait is and how environmental differences might affect them. Lundström (1963) analysed differences in cusp number, fissure patterns, crown form, and lingual variations of the anterior teeth in order to asses zygosity in 70 twin pairs from Michigan and 54 pairs from New York. The results indicated that he diagnosed correctly a 91.7% of monozygotic twins and a 98.1% of the dizygotic ones. In a similar study, Townsend and collaborators (1988) diagnosed the zygosity of 120 pairs of Australian white twins with 97.5% accuracy. Moreover, in a study of monozygotic twins separated at birth (and consequently growing on different conditions), high concordance of expression of the different dental traits was described (Boraas *et al.*, 1988). Townsend and collaborators (2009 b) suggest a high heritability of dental measurements, inter-cusp distance and Carabelli's trait on a model simulation study on twins, while other occlusal features like overbite and overjet show low genetic inheritance.

In summary, dental non-metric traits show a high inheritance pattern, characterised by a multigenic interaction determining the traits that follows neither simple Mendelian inheritance nor a complex segregation model. Furthermore, even if some individuals might be more affected by environmental factors interacting in dental development, this effect is minimal and the impact on population frequencies would not be significant (Scott & Turner, 1997).

The amount of researchers including analysis of dental morphology in their works, and the number of anthropological and archaeological questions that have been addressed analysing the non-metric dental traits have increased since the implantation of the standardized recording system. Some of these problems that have been studying with this methodology are: the ethnic affiliation of the first Egyptians (Irish, 2006); the origin of agricultural groups, and relationships between culturally different prehistoric groups in Italy (Coppa *et al.*, 2007; Cuccina *et al.*, 1999); the relationship among Eastern Asian populations, for example the different Japanese populations, or Neolithic Chinese populations (Manabe *et al.*, 2003; 2011); the development of the Campaniform or Bell-Beaker culture in Europe (Desideri, 2007); the relationship between Sub-Saharan and North-African populations (Irish, 1998). The utilisation of dental morphology has also increased in the anthropology departments of Spain too by for example its use to characterise Muslim remains from Al-Andalus period (Laguillo *et al.*, 2009) or the study of the interactions between Balearic islanders and continental groups (García-Sivoli, 2009).

2. OBJECTIVES

The main goal of this thesis is to reconstruct the biological variability on the populations involved in the transition from the Mesolithic to the Neolithic in the northeast of the Iberian Peninsula by the analysis of their dental morphology, a methodology that allows the incorporation of big samples. In order to achieve this aim, the following specific objectives have been established:

1. Understanding the variability in dental morphology and the influence environmental stress might have on the phenotype.

2. Characterising the Mesolithic and Neolithic groups from the Iberian Peninsula by means of dental morphology.

    1. Testing the biological homogeneity of the different Neolithic groups from the northeast of the Iberian Peninsula: focusing on the chronology, geographical dispersion of the groups and the cultural variability during the period.
    2. Testing the biological homogeneity of the Mesolithic samples from different areas of the Iberian Peninsula.

3. Analysing the biological affinities between Mesolithic and Neolithic groups of the northeast of the Iberian Peninsula and surrounding areas.

3. MATERIALS & METHODS

3.1. MATERIALS

The sites studied to achieve these objectives represent the various chronological periods and geographical areas involved in the transition from a hunter-gatherer to a productive economy in the northeast of the Iberian Peninsula were studied. The periods included in this study therefore are: the Upper Palaeolithic, Mesolithic, Neolithic (Early, Middle and Late) and Early Bronze Age. Inside the northeast of the Peninsula, the sites represent the Cantabrian Fringe, Ebro basin and Catalan territory. Moreover, in the case of Mesolithic samples some sites from Portugal and Valencia have also been included. Finally, Neolithic samples from southern France have also been considered in order to estimate the role of the Pyreneans as a barrier or a passageway.

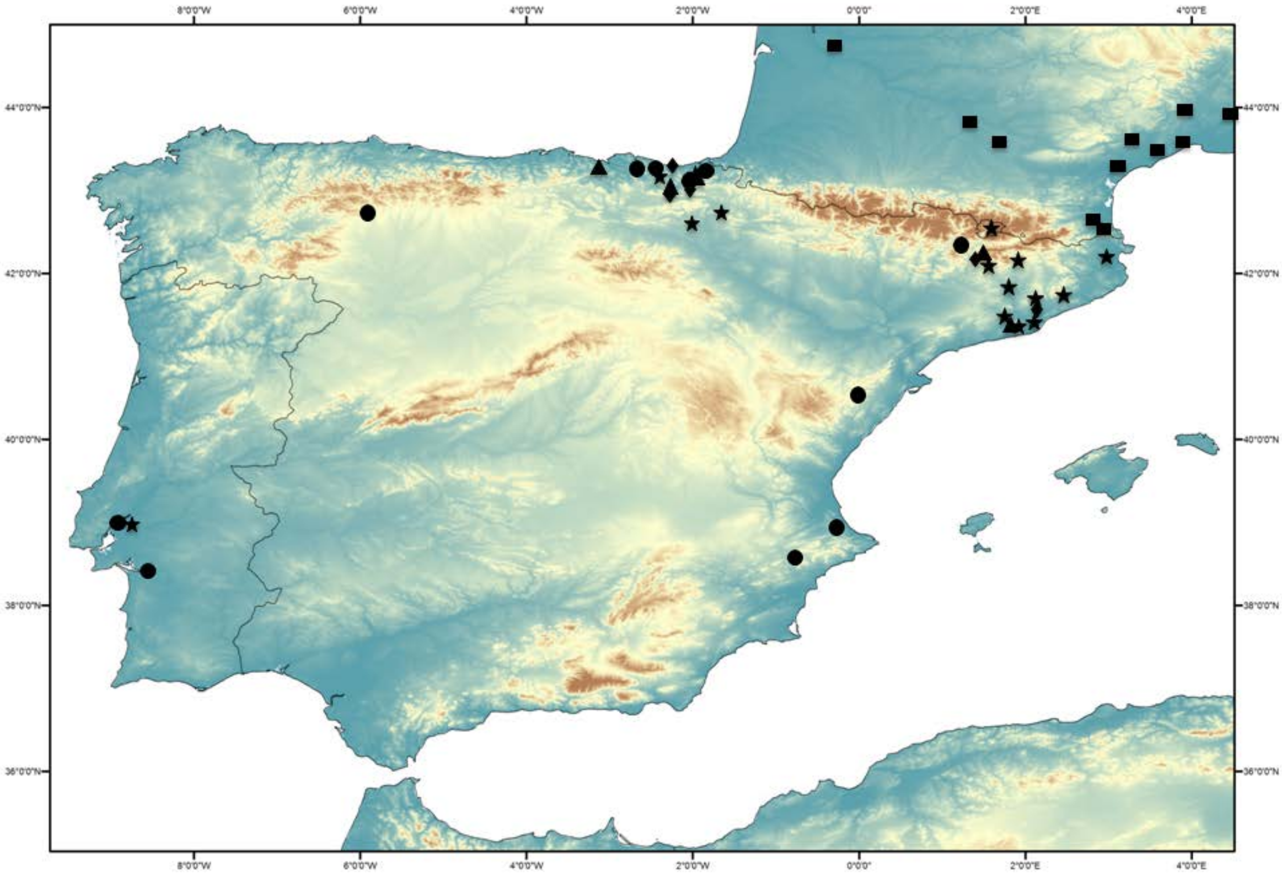

Figure 18. Map that shows the location of the 96 sites included in the study. Dots: Hunter Gatherers; Stars: Early- and Middle-Neolithic Samples; Triangles: Chalcolithic Samples; Diamonds: Bronze-Age Samples; Squares: Middle- and Late- Neolithic French samples. (Base map generated by Gerard Remolins).

This study involved a total amount of 100 sites (Figure 18). And as a whole, the minimum number of individuals studied between all these archaeological sites sums up to 1,391, and the total amount of studied teeth is 17,262.

3.1.1. Upper Palaeolithic samples

Isolated teeth from four Magdalenian sites have been analysed for this work, three caves and a rock-sheltter (Table 4; Figure 19). The sites that conform this sample are: Santimamiñe and Santacatalina caves in Biscay (Albisu *et al.*, 2014; Herrasti & Etxebarria, 2011); Erralla cave in Gipuzkoa (Altuna *et al.*, 1985); Balma Guilanyà (Subirà et al., 2009) in the province of Lleida; and Cingle de l'Aigua (Román-Monroig, 2010) in Castellon. Between all of them they comprise a total amount 7 individuals and 17 teeth.

Table 4. List of Upper Palaeolithic samples included in the work. The numbers coincide with those in Figure 19.

Site	Name	Chronology/Date	Type of site	Geographical area	References	NMI	Number of teeth
1	Santimamiñe	Magdalenian	Cave	Biscay	Herrasti & Etxebarria, 2011; López-Quintana & Guenaga-Lizasu, 2011	1	2
2	Santa Catalina	11,212-10,851 cal BCE	Cave	Biscay	Albisu *et al.* , 2014; Berganza-Gochi & Arribas-Pastor,2014	1	1
3	Erralla	Magdalenian	Cave	Gipuzkoa	Altuna *et al.* , 1985	1	2
4	Balma Guilànya	11,811-10,877 cal BCE	Rock-Sheltter	Lleida	Subirà *et al.* , 2009 a	3	10
5	Cingle de l'Aigua	10,711-10,211 cal BCE	Rock-Sheltter	Castellón	Román-Monroig, 2010	1	2
						7	17

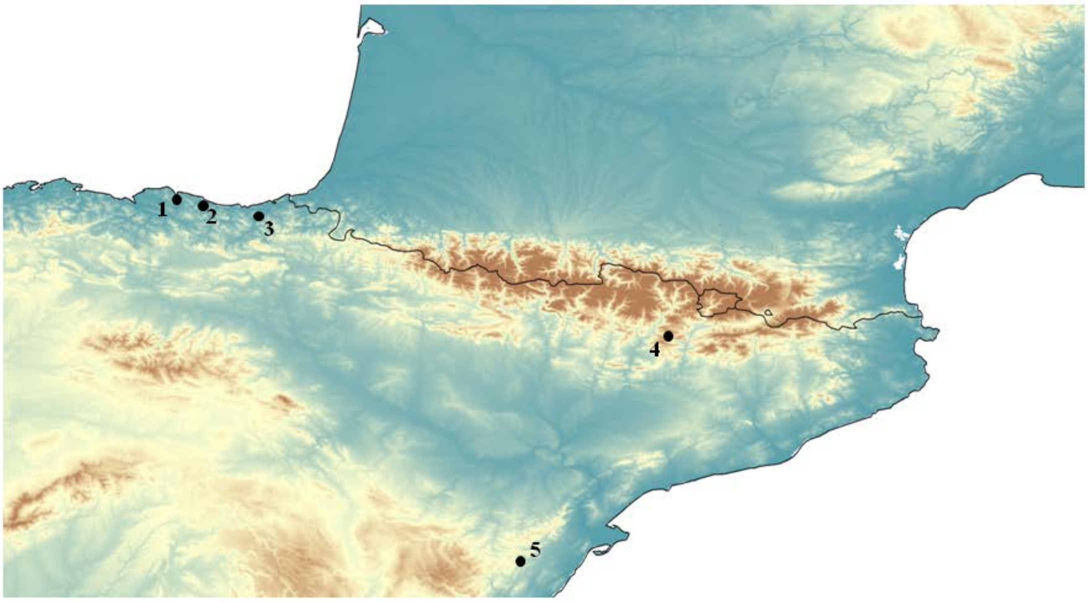

Figure 19. Map showing the location of the 4 Upper-Palaeolithic samples included in the work. The names of the sites are shown in Table 4. (Base map generated by Gerard Remolins).

3.1.2. Mesolithic samples

As it has been mentioned in the introduction, during the Mesolithic, the amount of funerary representations increased compared to the previous period. Nevertheless, there are few sites in the Iberian Peninsula where more than two individuals were buried during the Mesolithic (Figure 2), and the larger ones are found in the Portuguese estuaries. In this work we have studied Mesolithic samples from three main areas of the Peninsula: the Mediterranean coast, the northern area (Cantabrian coast and inland), and the rock-sheltters from Muge and Sado estuaries in Portugal (Table 5; Figure 20). Although these burials were done in a wide chronological frame, most of them concentrate in the Boreal period (8,700-7,500 BP), with the exception of some early burials from El Collado (Valencia), and late burials from the North (some of the burials related to Mesolithic contexts in this last area have been dated to 6,630 BP). In sum, the sample from this period was conformed by 317 individuals, at least, and 1,315 teeth.

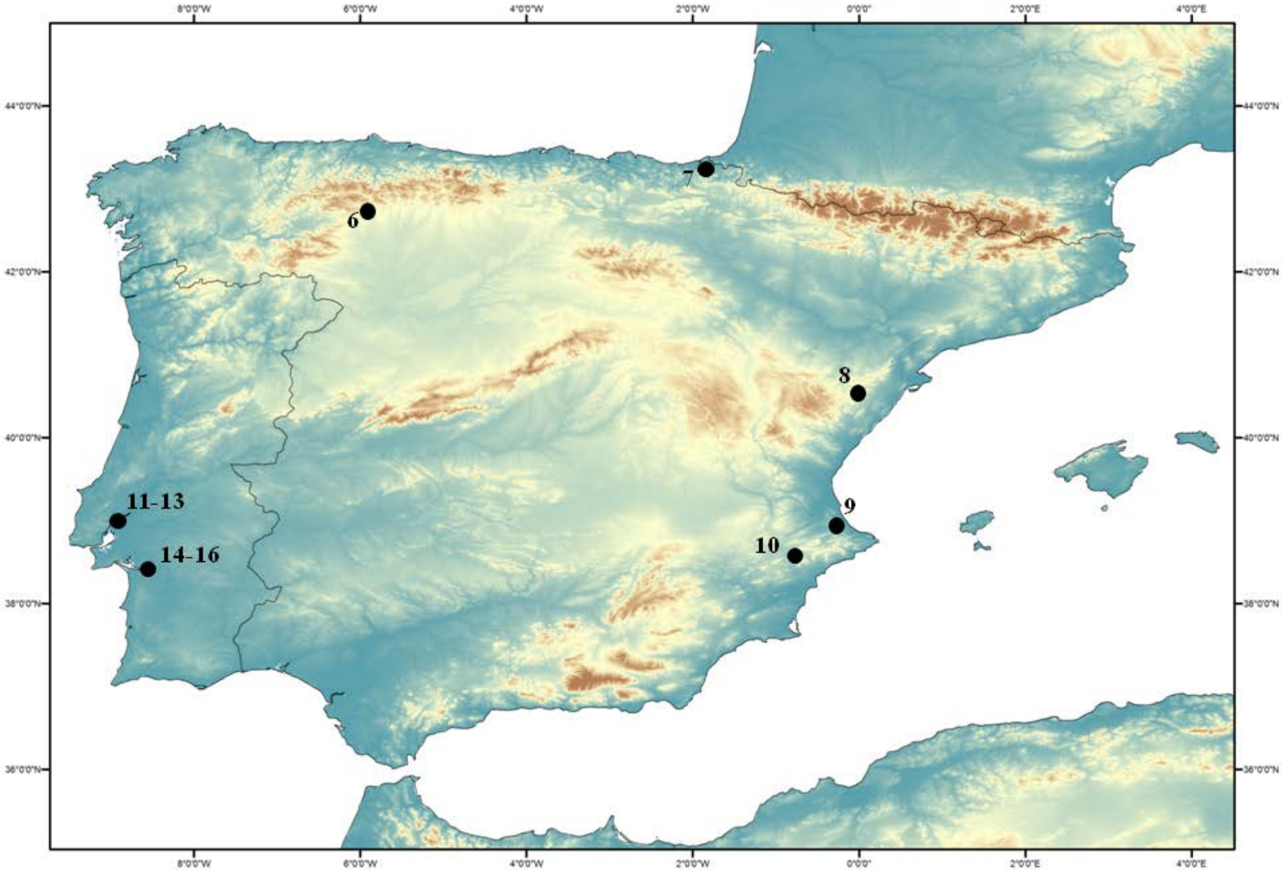

Figure 20. Map showing the location of the Mesolithic samples included in the work. The names of the sites are shown in Table 5. (Base map generated by Gerard Remolins).

Table 5. List of the Mesolithic samples included in the work.

Site	Name	Chronology/Date	Type of site	Geographical area	References	NMI	Number of teeth
6	La Braña	5,990-5,740 cal BCE; 6,010-5,800 cal BCE	Cave	Leon	Vidal-Encinas & Prada-Marcos,, 2010; Prada-Marcos, 2010	2	35
7	J3	7530-7180 cal BCE	Rock-Sheltter	Basque Country	Iriarte *et al.* , 2010	1	2
8	Cingle del Mas Nou	8007–7583 cal BP	Rock-Sheltter	Castellón	Olaria, 2010	2	15
9	El Collado	7,539-7,356 cal BCE - 6,642-6,486 cal BCE	Rock-Sheltter	Valencia	Campillo *et al.* , 2008; Gibaja *et al.* , 2015	15	73
10	Casa Corona	8007–7583 cal BP	Open-Air	Alicante	Fernández-López de Pablo *et al.* , 2013	3	20
11	Moita do Sebastiao	6,200- 5,450 cal BCE	Rock-Sheltter	Muge Estuary (Portugal)	Jackes & Meiklejohn, 2008; Peyroteo-Stjerna, 2016	85	627
12	Cabeço da Arruda	6,100-4,900 cal BCE	Rock-Sheltter	Muge Estuary (Portugal)	Cunha & Cardoso, 2002-03; Roksandic, 2006; Peyroteo-Stjerna, 2016	110	382
13	Cabeço da Amoreira	6,050-5,200 cal BCE	Rock-Sheltter	Muge Estuary (Portugal)	Bicho *et al* ., 2013; Cunha & Cardoso, 2001; Roksandic, 2006; Peyroteo-Stjerna, 2016	29	37
14	Arapouco	6,232-5,713 cal BCE	Rock-Sheltter	Sado Estuary (Portugal)	Cunha & Umbelino, 1995-97; Peyroteo-Stjerna, 2016	32	15
15	Cabeço das Amoreiras	6,100-5,300 cal BCE	Rock-Sheltter	Sado Estuary (Portugal)	Cunha & Umbelino, 1995-97; Peyroteo-Stjerna, 2016	6	26
16	Cabeço do Pez	5,800-5,400 cal BCE	Rock-Sheltter	Sado Estuary (Portugal)	Cunha & Umbelino, 1995-97; Peyroteo-Stjerna, 2016	32-36	83
						317-321	1,315

3.1.3. Early and Middle Neolithic samples

During the Early Neolithic and especially, the Middle Neolithic, open-air burials flourished in the Northeast of the Iberian Peninsula. The most extended form of burial in this period was that based pits excavated on the soil, usually forming Necropolis. Moreover, in the Pre-Pyrenean area of el Solsonés (Barcelona) and the Pyrenees individuals were buried in tombs created with stone slabs, called cists. In the Atlantic area of Basque Country the few Middle Neolithic burials found to date appear in caves and isolated.

Samples of the three representations were included in this study (Table 6, Figure 21): the Early Neolithic sample from Plaça de la Villa de Madrid (Barcelona); 20 sites included in the Pit Burials (Sepulcres de Fossa) tradition from Catalonia; 18 cist burials from the Pre-Pyrenean and Pyrenean areas; Los Cascajos and Paternanbidea Early-Neolithic open-air sites from Navarre (Los Cascajos has both Early- and Middle-Neolithic burials); and Marizulo and Lumentxa caves from the Atlantic Basque Country. The burial in Marizulo, although inside a cave, was done inside a stone cist (Figure 22). The remains from Algar do Bom Santo (Muge estuary, Portugal) were also analysed. The sample from this period consists of at least 449 individuals and 5,792 teeth, from 43 sites.

3.1.4. Chalcolithic samples

The Chalcolithic samples studied for this work consisted of burials in collective graves, both sepulchral caves and megalithic monuments. While the megalithic structures varied in size, shape and typology depending on the geographic location, the characteristics of the sepulchral caves were homogeneous along the territory. Therefore, megaliths from the Atlantic basin of the Basque Country and Solsonian area were studied. Meanwhile, caves from Mediterranean areas, Pre-Pyrenean areas and Atlantic areas were included in the work. The samples accounted from 14 sites (5 Megaliths and 9 Caves) and included 239 individuals at least and 4,200 teeth (Table 7, Figure 23).

Table 6. List of the Early- and Middle-Neolithic samples included in the work.

Site	Name	Chronology/Date	Type of site	Geographical area	References	NMI	Number of teeth
17	Lumentxa	Middle Neolithic	Cave	Biscay	Arribas-Pastor, *personal comunication*	1	12
18	Marizulo	Middle Neolithic	Cave	Gipuzkoa	Laborde *et al.* , 1967	1	14
19	Los Cascajos	5,140-3,880 cal BCE	Open-Air	Navarre	García & Sesma, 2001; García & Sesma, 2007; García-Gazolaz *et al.* , 2011	27	394
20	Paternanbidea	5,000-4,850 cal BCE	Open-Air	Navarre	García, 2007	9	105
21	Segudet	4,323-4,052 cal BCE	Cist	Andorra	Remolins *et al.* , 2016	1	15
22	Feixa del Moro	3,978-3,787 cal BCE; 3,946,3,710 cal BCE	Cist	Andorra	Remolins *et al.* , 2016	1	13
23	Can Ignasi	Neolithic	Cist	Solsonès	Fígols, 1996	1	4
24	Cementiri de Solsona	Neolithic	Cist	Solsonès	Fígols, 1996	1	9
25	Ceuró I, II	3,941-3,666 cal BCE; 3,909-3,657 cal BCE	Cist	Solsonès	Morell *et al.* , in press b	3	46
26	Cista de la Puput	Neolithic	Cist	Solsonès	Lorencio C, Xandri J, Canela M. 1983	1	7
27	Colilles	Neolithic	Cist	Solsonès		2	24
28	Costa dels Garrics del Caballol I, II	3,943-3,638 cal BCE; 3,760-3,526 cal BCE; 3,634-3,375 cal BCE; 3,635-3,376 cal BCE	Cist	Solsonès	Castany, 1991; Morell *et al.* , in press b	3	71
29	El Llord I, II, V	3,340-2,575 cal BCE	Cist	Solsonès	Castany, 2009	5	87
30	El Megalit del Senyor Bisbe	3,975-3,800 cal BCE	Cist	Solsonès	Morell *et al.* , in press b	1	24
31	El Vilar de Simosa	3,931-3,665 cal BC	Cist	Solsonès	Morell *et al.* , in press b	4	99
32	Estació del Solar III	3,926-3,661 cal BCE; 3,930-3,664 cal BCE	Cist	Solsonès	Morell *et al.* , in press b	2	23
33	Fossa del Camí dels Casals	Neolithic	Cist	Solsonès	Castany i Guerrero 1989	1	6
34	Les Censades	Neolithic	Cist	Solsonès	Serra Vilaró, 1927	2	27
35	Palà de Coma I, II	3,785-3,364 cal BCE	Cist	Solsonès	Fígols, 1996	3	42
36	Cal Tururut	Neolithic	Cist	Solsonès	Castany i Guerrero 1983-84	1	3
37	Tomba del Moro de Sorba	3,895-3,655 cal BCE	Cist	Solsonès	Morell *et al.* , in press	2	25
38	Boixadera dels Bancs	Neolithic	Sepulchral cave	Solsonès	Serra Vilaró, 1927	16	131
39	Canal dels Avellaners	V-IV millenium cal BCE	Reuse of the chanel	Berguedà	Carreras, 1990, Gibaja *et al.* , 2015	1	13
40	Corral de Canudas	initial IV millenium cal BCE	Cist	Berguedà	Gibaja *et al.* , 2015	1	18
41	Serrat de les tombes	final IV millenium cal BCE	Cist	Berguedà	Servei d'Arqueologia del Berguedà (comunicació personal)	2	46
42	Pla del Riu de les Marcetes	3,781-3,650 cal BCE	Pit Burials	Manresa	Guitart i Perarnau, 1986; Oms *et al.* , 2016	1	28
43	Can Gelats	initial IV millenium cal BCE	Pit Burials	Girona	Gibaja *et al.* , 2016	1	29
44	Hort d'en Grimau	52750-5270	Pit Burials	Penedès	Mestres, 1988-1989; Oms *et al.* , 2016	3	35
45	Pujolet de Moja	3,946-3,656 cal BCE	Pit Burials	Penedès	Mestres *et al.* , 1997; Oms *et al.* , 2016	3	90
46	Eix Diagonal	V-IV millenium cal BCE	Pit Burials	Penedès	servei d'arqueologia de Catalunya	11	179
47	Mas d'en Boixos	4825-4915 cal BC	Pit Burials	Penedès	Bouso *et al.* , 2004, Oms *et al.* , 2016	5	81
48	Can Tintorer	IV millenium cal BCE	Pit Burials	Garraf	Oms *et al.* , 2016; Villalba, 1999; Villar *et al.* , 2011	35	324
49	C/ Pi 11	initial IV millenium cal BCE	Pit Burials	Barcelona	Cebrià *et al.* , 2016	2	38
50	Plaça de la Vila de Madrid	5,479-5,331 cal BCE	Pit Burial	Barcelona	Pou *et al.* , 2010	1	16
51	La Gardunya	4000-3936 cal BCE	Pit Burial	Barcelona	Montes *et al.* , 2014, Velasco, 2016	1	20
52	Filmoteca	4000 - 3300/3200 a.C	Pit Burial	Barcelona	Nadal & Castillo, 2010, Ruiz *et al.* , 2010	1	28
53	Can Gambus	3800-3495 cal BC	Pit Burials	Vallès	Roig *et a.* ,l 2010; Villar *et al.* , 2006	27	420
54	Bòbila Madurell	4730-4890 cal BC	Pit Burials	Vallès	Oms *et al.* , 2016	102	1,303
55	Can Roqueta Can Revella	final V- initial IV millenium cal BCE	Pit Burials	Vallès	Morell *et al.* , in press a	3	45
56	Can Vinyals	5130-5220 cal BC	Pit Burial	Vallès	Bouso *et al.* , 2004, Oms *et al.* , 2016	3	66
57	Can Soldevilla	V-IV millenium cal BCE	Pit Burial	Vallès	Miquel i Serra & Morral, 1980	1	6
58	Camí de Can Grau	V-IV millenium cal BCE	Pit Burial	Vallès	Costa *et al.* , 1982	36	693
59	Algar do Bom Santo			Muge	Duarte, 1998	121	1,133
						449	5,792

Table 7. List of the Chalcolithic samples included in the work.

Site	Name	Chronology/Date	Type of site	Geographical area	References	NMI	Number of teeth
60	Pico Ramos	3,911-3,346; 3,091-2,486; 2,913-2,347 cal BCE	Sepulchral cave	Biscay	Zapata, 1995 b	104	2,294
61	Argarbi	Chalcolithic	Megalith	Gipuzkoa	Mujika & Edeso, 2012	12	180
62	Gorostiaran Oeste	Chalcolithic	Megalith	Gipuzkoa	Aranzadi *et al.* , 1919; Mujika & Edeso, 2012	4	74
63	Gorostiaran Este	Chalcolithic	Megalith	Gipuzkoa	Aranzadi *et al.* , 1919; Mujika & Edeso, 2012	4	74
64	L'Atalaia A	Chalcolithic	Sepulchral cave	Solsonès		1	6
65	Balma de Garrigó	Chalcolithic	Sepulchral cave	Solsonès		2	17
66	Espluga Negra	Chalcolithic	Megalithic sepulchral cave	Solsonès	Serra-Vilarò, 1927	5	34
67	Caixa del Moro de Castelló	Chalcolithic	Megalithic cist	Solsonès	Serra-Vilarò, 1927	10	74
68	Corderoure	Chalcolithic	Megalithic sepulchral cave	Solsonès	Serra-Vilarò, 1927	2	20
69	Roca dels Moros de Finestres	Chalcolithic	Megalithic sepulchral cave	Solsonès	Serra-Vilarò, 1927	11	67
70	La Pera	Chalcolithic	Megalith	Solsonès	Serra-Vilarò, 1927	3	9
71	Llera BB	Chalcolithic	Sepulchral cave	Solsonès	Serra-Vilarò, 1927	1	2
72	Can Sadurní (Capa 9)	4135-4315 cal BCE	Sepulchral cave	Garraf	Edo *et al.* , 1982, Oms *et al.* , 2016	50	1,028
73	Cova del Pantà de Foix	3,420-2,640 cal BCE	Sepulchral cave	Garraf	Cebrià *et al.* , 2013	30	321
						239	4,200

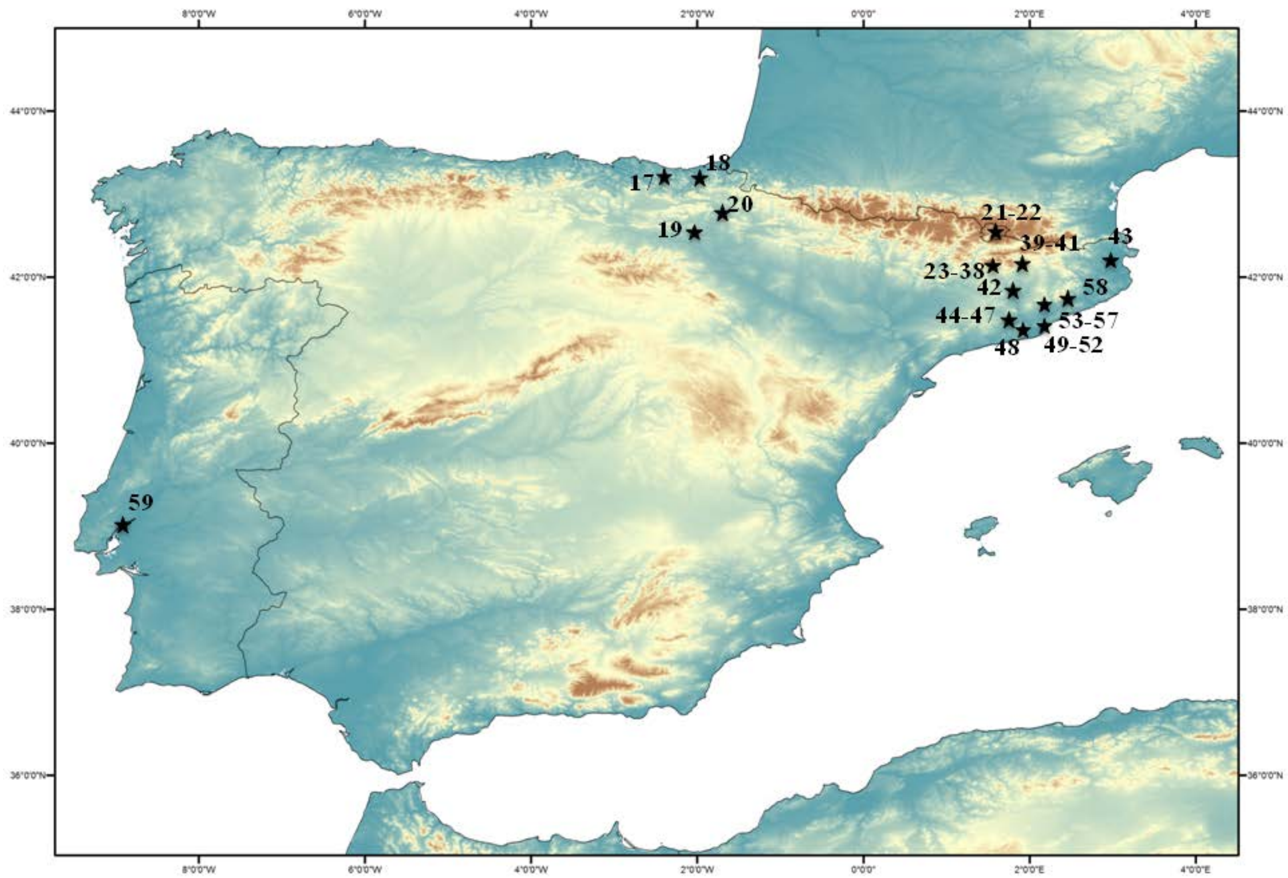

Figure 21. Location of the different Early- and Middle-Neolithic sites included in the work. The numbers regarding the sites coincide with those in table 6. (Base map generated by Gerard Remolins).

Figure 22. Scheme of Marizulo's burial in a cist inside the cave. (Laborde *et al.*, 1967).

3.1.5. Bronze Age samples

In order to understand the biological outcome of the interactions occurred during the development of the Neolithic, including the exchange networks and latter migrations, some Bronze Age contexts were included in the work. The studied samples covered Urtiaga, Pikandita and Iruaxpe I caves in

Deba (Basque Country), the tumulus Pinetons in Ripollet (Barcelona), and 11 Catalan Pre-Pyrenean sites including caves, tumulus and dolmenic structures (Table 8, Figure 24). The minimum number of individuals and teeth recovered from these sites reached 119 and 1,494 respectively.

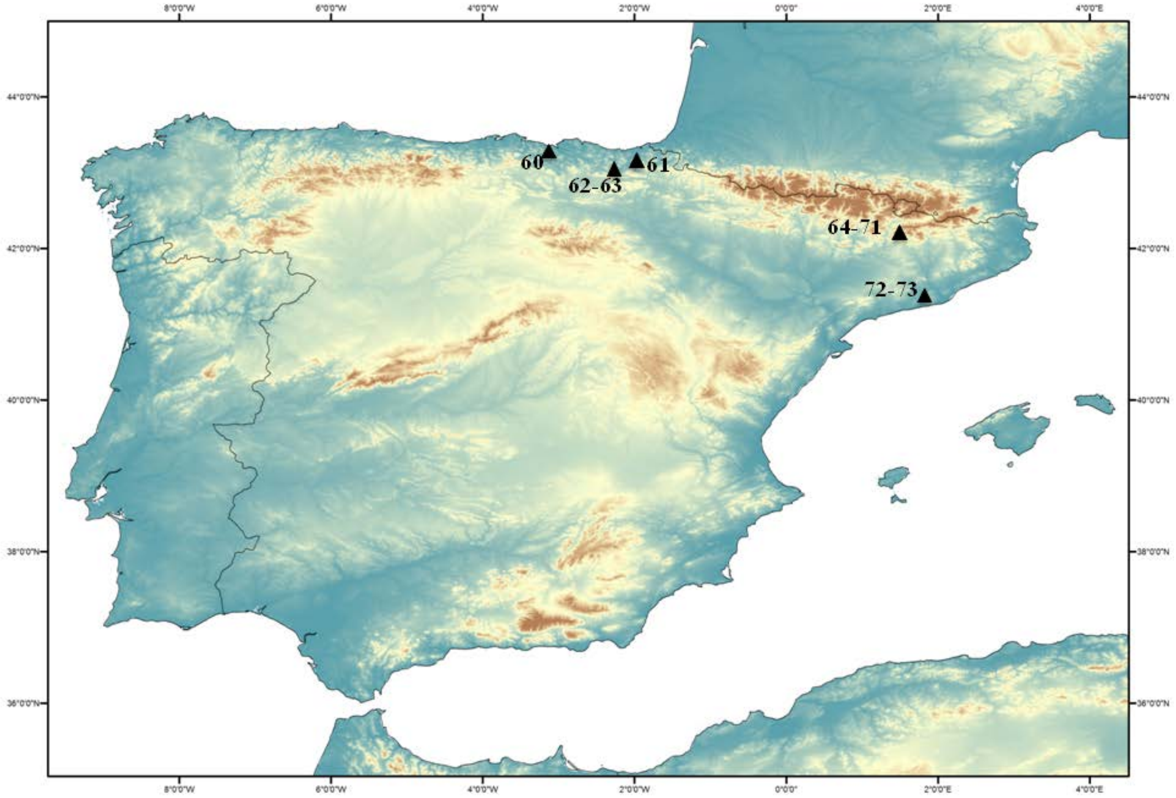

Figure 23. Location of the different Chalcolithic sites included in the work. The numbers of the sites coincide with those in table 7. (Base map generated by Gerard Remolins).

3.1.6. French samples for comparison

French Neolithic samples were also studied in order to have some control groups outside the Peninsula. This group was selected because of geographic closeness and the many cultural affinities between the Neolithic groups at both sides of the Pyrenean mountains (Vaquer *et al.*, 1990). The 12 samples are representative of Middle Neolithic groups from Provence (Les Martins, Saint Maximin and Collet Redon), Languedoc and the Roussillon (Le Crés, La Terrasse, Villeneuve-Tolosane/ La Vimona et Zac Agora, Cugnaux, Narbons, Rouergàs, Bellesta and Montou) areas, and late Neolithic from Provence (Roaix) and Aquitania (Grôtte Mykolas) (Figure 24). As indicated in Table 9 the minimum number of individuals studied in these sites is 260 and they comprise 4,444 teeth.

Table 8. List of the Bronze-Age samples included in the work.

Site	Name	Chronology/Date	Type of site	Geographical area	References	NMI	Number of teeth
74	Urtiaga	1,800-1,740 cal BCE	Cave	Gipuzkoa	Altuna & de la Rúa, 1989	25	587
75	Iruaxpe I	Bronze Age	Cave	Gipuzkoa	Altuna *et al.* , 1995	15	320
76	Pikandita	Bronze Age	Cave	Gipuzkoa	Altuna *et al.* , 1995; Armendariz & Etxeberria, 1983	4	58
77	Ceuró III	2,022-1,7778 cal BCE	Cist	Solsonès	López-Onaindia *et al.* , 2017	1	7
78	Altaracs I	1,623-1,461 cal BCE	Cist	Solsonès	López-Onaindia *et al.* , 2017	1	8
79	Coïns	Bronze Age	Cist	Solsonès	inventari patrimoni arqueològic de la Generalitat	2	9
80	Cova de Sant Bartomeu	Bronze Age	Cave	Solsonès	Soriano, 2013	9	36
81	Forat de la Tuta	1,739-1,508 cal BCE	Cave	Solsonès	Soriano, 2011	1	5
82	Dolmen de Clarà	909-798 cal BCE	megalith	Solsonès	Museu Diocesal i Comarcal de Solsona; Castany, 1991	3	12
83	Santes Masses	2,141-1,882 cal BCE	Cist	Solsonès	Castany et al., 1994, inventari Patrimoni Arqueològic de Catalunya	2	36
84	Collet de les Forques	Bronze Age	megalith	Solsonès	Serra Vilaró, 1927	4	40
85	La Guàrdia	Bronze Age	Tumulus	Solsonès	Crònica de la Secció Arqueològica. 1915-1920	1	13
86	Collet de Saltzer I	Bronze Age	Megalith	Solsonès	Baulenas *et al.* , 2008	2	12
87	Aigües Vives	1,880-1,330 cal BCE	Paradolmen	Solsonès	Castany, 1991; Pedro, 2008	9	72
88	Els Pinetons	III millenium BCE	Tumulus	Vallès	Balsera *et al.* , 2010	40	279
						119	1,494

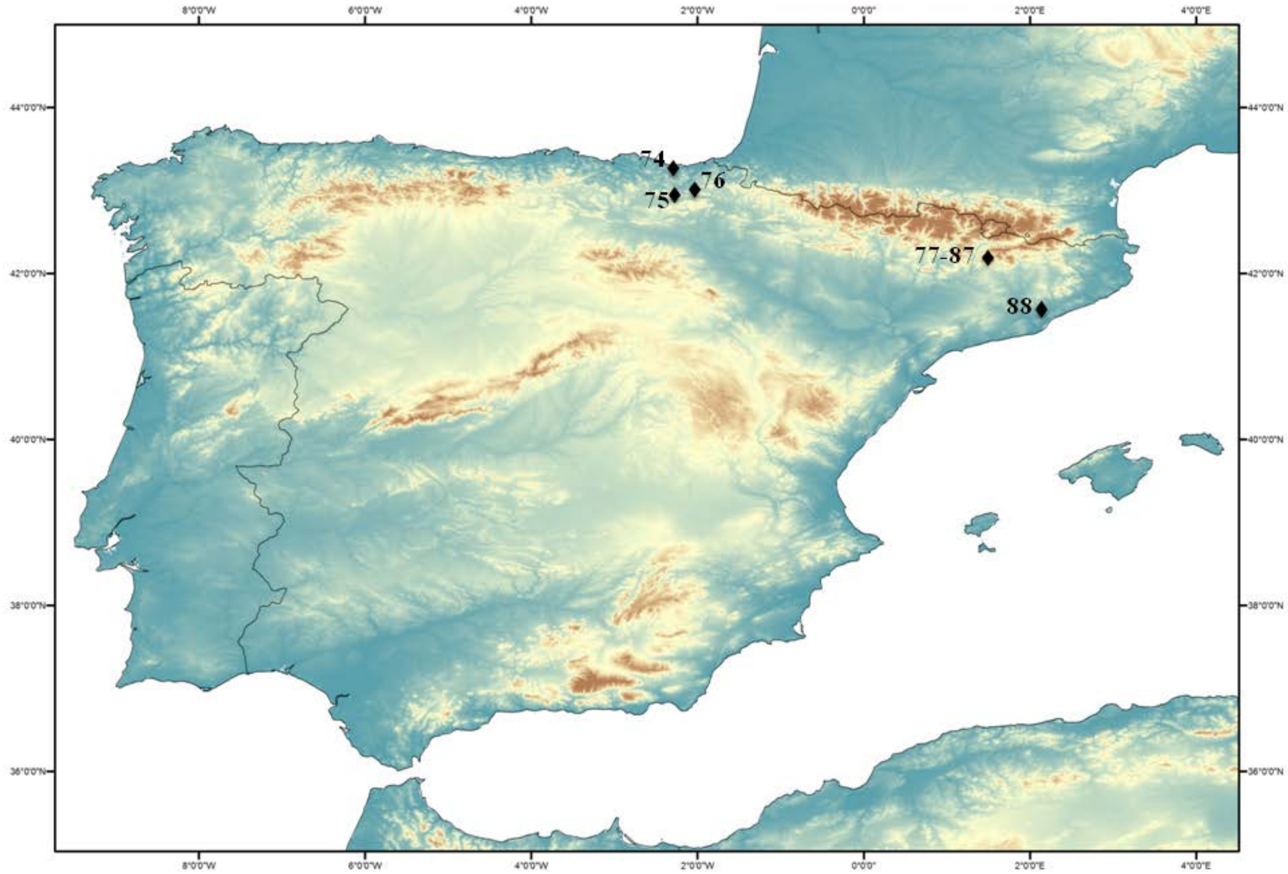

Figure 24. Location of the different Bronze-Age sites included in the work. The numbers of the sites coincide with those in table 8. (Base map generated by Gerard Remolins).

Moreover, some other sites or remains from some of the included sites have been studied. Nevertheless, these have not been included in the study due to lack of dates and reliable contexts, which does not allow us to group them neither in the Chalcolithic group nor in the Bronze Age group. The samples include individuals from Lumentxa and Santimamiñe caves, as well as the whole ensemble from Abittaga, Atxuri, and Txotxinkoba caves, all of them from Biscay.

Table 9. List of the French Neolithic samples included in the work.

Site	Name	Chronology/Date	Type of site	Geographical area	References	NMI	Number of teeth
89	Grôtte Mykolas	Late Neolithic/Chalcolithic	Cave	Aquitania	Chancerel *et al.* , 2007	12	256
90	La Terrase, Villeneuve-Tolosane/ La Vimona et Zag Agora, Cugnaux	4,200-3,800 cal BC	Pit Burials	Midi-Pyrenees/Languedoc	Gandelin & Vaquer, 2008	10	183
91	Narbons	4,248-3,3369 cal BC	Pit Burials	Midi-Pyrenees/Languedoc	Tchéremissinof *et al.* , 2005	3	71
92	Caune de Bèlesta	Early/Middle-Neolithic	Cave	Rousillon	Claustre *et al.* , 1993	10	54
93	Montou	Early/Middle-Neolithic	Cave	Rousillon	Claustre & Ponsich, 2000; Valentin *et al.* , 2003	8	143
94	Le Crés	End of V millennium BCE	Pits and Cists	Languedoc-Rousillon	Loison *et al.* , 2004; Loison & Schmitt, 2009	39	467
95	Rouergas	IV millennium BCE	Pit Burials	Languedoc-Rousillon	Vignaud et al., 1997	4	11
96	Les Martins	Beggining of IV millennium BC	Pit Burials	Provence	D'Anna et al., 1993	2	40
97	Les Clavelles, Lurs	V-IV millenium BCE	Pit Burials	Provence	Schmitt, personal comunication	4	36
98	Collet Redon	IV millennium BCE	Pit Burials	Provence	Schmitt *et al.* , in press b	6	116
99	Roaix (Couche 5)	End of IV millennium BCE	Hypogeum	Provence	Courtin, 1974; Sauzade, 1983	159	2,994
100	Saint Màximin	V millennium BCE	Pit Burials	Provence	Remicourt *et al.* , 2014; Schmitt *et al.* , in press a	3	73
						260	4,444

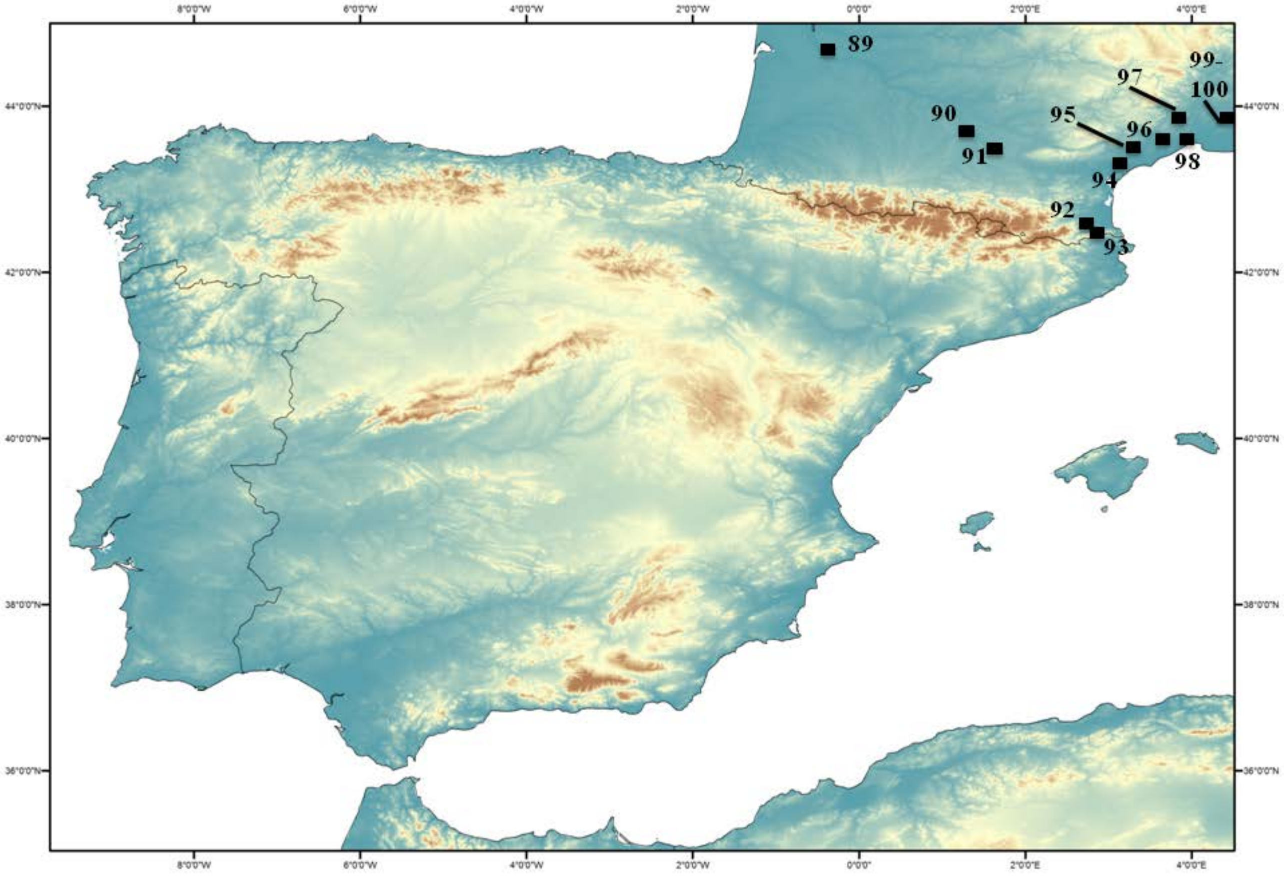

Figure 25. Location of the French Neolithic sites included in the work. The numbers of the sites coincide with those in table 9. (Base map generated by Gerard Remolins).

3.2. METHODOLOGY

3.2.1. Scoring the data and pre-analysis preparation of the raw data

The recollection of the morphological traits from dental crown and roots was carried out following the ASUDAS methodology (Arizona State University Dental Anthropology System) (Turner *et al.*, 1991). This methodology standardises the observation of the nonmetric traits so that they can be easily replicable between researchers and in different samples, and provides plaques representing different expression levels that can show each trait (Figure 26). These traits include the number of cusps and roots, as well as tubercles, grooves and ridges present in the dental crown and root. Therefore, these plaques showing the different expression levels that each trait can show are useful due to the diversity of shapes that can be present. In sum, the authors provide the standards to score 35 traits that, taking into account that some of them might be observed in more than a single tooth, correspond to 121 variables in a full dentition (Table 10).

The observation of most traits was qualitative at bare-sight, although a couple traits have intermediate stages that require measuring concrete diameters of the teeth (Figure 26). Moreover, X-ray based computed tomographies were conducted on the specimens in the cases when radiographic images were necessary for determining the nature of extreme variation and the absence of determinate teeth (when it was possible).

For most of the statistical analyses that were carried out, the data must be treated beforehand. The only exception when the raw data was used as recorded was for the analysis of the fluctuating asymmetry, where the aim was to compare the expression of the traits between both antimers. For the rest of the analyses carried out in this work it was necessary to select one of the antimers in each tooth pair. This is necessary in order to have the same representation for each individual that is analysed, because in many cases archaeological remains lack a semiarcade or some teeth. The antimer that was chosen was the one presenting the highest level of expression for the traits, as this is considered an indicator of a major genetic potential (Scott & Turner, 1997; Turner *et al.*, 1991).

Once the most genetically reliable antimer was selected the scalated data were dichotomised into presence/absence values using the dichotomic breaking points proposed by Coppa and collaborators (2007), Scott and Turner (1997), and Turner and collaborators (1991) in order to have available data from prehistoric European samples that could be compared.

Finally, traits were edited in order to prevent from using traits that were 1) not informative: for example, a trait that is present in the same frequency or absent in all the analysed samples; and 2) correlated traits: in the case that correlation between traits could be detected one of the traits of the correlated pair was eliminated in order to avoid differential weighting of the underlying dimensions that might yield erroneous results (Irish, 2010; Sjøvold, 1977).

3.2.2. Statistical analyses

Several statistical methods where applied in order to analyse the obtained data and the biological diversity and affinities within and between the different samples. The analyses were focused on determining the fluctuating asymmetry presented in the individuals from different samples, the correlation in the expression of different traits, the determination of differences in the presence of concrete traits between the various samples, and the determination of biological affinities between the samples.

3.2.2.1. Analysis of the fluctuating asymmetry

Fluctuating asymmetry (FA) is often considered a measure of developmental instability. In this work, FA was studied in order to test the possible environmental origin of the malformations observed in some of the samples. Raw and scaled data was used to calculate the proportions of asymmetric individuals (Marado *et al.*, 2016). Moreover, Kendall’s Tau-b correlation coefficient was calculated with SPSS 20.00 to determine the nature of antimere asymmetries. Directional asymmetry should result in weak correlations (both positive or negative); antisymmetry should provide moderate to strong negative associations; finally fluctuating asymmetry should result in moderate to very strong positive associations.

Table 10. The 121 variables scored in a full dentition following the ASUDAS methodology.

Maxillary		**Mandibular**	
Anterior teeth	*Posterior teeth*	*Anterior teeth*	*Posterior teeth*
UI1 Winging	UP3 Double Shoveling	LI1 Shoveling	LP3 Lingual Cusps
UI1 Labial Curve	UP3 Distossagital Ridge	LI1 Double Shoveling	LP3 Enamel Extension
UI1 Interruption Groove	UP3 m&d Cusps	LI1 Root Number	LP3 Root Number
UI1 Shoveling	UP3 Enamel Extension	LI1 Radical	LP3 Radical
UI1 Double Shoveling	UP3 Root Number	LI1 Congenital Absence	LP3 Tomes' Root
UI1 Tuberculum Dentale	UP3 Radical	LI2 Shoveling	LP3 Odontome
UI1 Root Number	UP3 Odontome	LI2 Double Shoveling	LP4 Lingual Cusps
UI1 Radical	UP4 m&d Cusps	LI2 Root Number	LP4 Enamel Extension
UI2 Interruption Groove	UP4 Enamel Extension	LI2 Radical	LP4 Root Number
UI2 Shoveling	UP4 Root Number	LC Distal Accessory Ridge	LP4 Radical
UI2 Double Shovelling	UP4 Radical	LC Root Number	LP4 Odontome
UI2 Tuberculum Dentale	UP4 Odontome	LC Radical	LP4 Congenital Absence
UI2 Root Number	UP4 Congenital Absence		LM1 Groove Pattern
UI2Radical	UM1 Metacone		LM1 Cusp Number
UI2 Peg Shaped/Reduced	UM1 Hypocone		LM1 Defflecting Wrinkle
UI2 Congenital Absence	UM1 Cusp5		LM1 Distal Crest
UC Shoveling	UM1 Carabelli's Tubercle		LM1 Protostylid
UC Double Shoveling	UM1 C2 Parastyle		LM1 Cusp5
UC Tuberculum dentale	UM1 Enamel Extension		LM1 Cusp6
UC Mesial Ridge	UM1 Root Number		LM1 Cusp7
UC Distal Accessory Ridge	UM1 Radical		LM1 Enamel Extension
UC Root Number	UM2 Metacone		LM1 Root Number
UC Radical	UM2 Hypocone		LM1 Radical
	UM2 Cusp5		LM2 Groove Pattern
	UM2 Carabelli's Tubercle		LM2 Cusp Number
	UM2 C2 Parastyle		LM2 Defflecting Wrinkle
	UM2 Enamel		LM2 Distal Crest
	UM2 Root Number		LM2 Protostylid
	UM2 Radical		LM2 Cusp5
	UM3 Metacone		LM2 Cusp6
	UM3 Hypocone		LM2 Cusp7
	UM3 Cusp5		LM2 Enamel Extension
	UM3 Carabelli's Tubercle		LM2 Root Number
	UM3 C2 Parastyle		LM2 Radical
	UM3 Enamel		LM3 Groove Pattern
	UM3 Root Number		LM3 Cusp Number
	UM3 Radical		LM3 Defflecting Wrinkle
	UM3 Reduced		LM3 Distal Crest
	UM3 Congenital Absence		LM3 Protostylid
			LM3 Cusp5
			LM3 Cusp6
			LM3 Cusp7
			LM3 Enamel Extension
			LM3 Root Number
			LM3 Radical
			LM3 Torsomolar Angle
			LM3 Congenital Absence

3.2.2.2. Analysis of inter-trait correlation

This analysis was carried out in the samples that presented individuals with complete or mainly complete dentitions. The statistical analysis used for this purpose was Kendall’s Tau-b (Irish, 2010). We considered a correlation as strong when the Tau-b value was superior to 0.5, and for it to be statistically significant we considered that the N must be >10 and the p value <0.05.

3.2.2.3. Analysis of single trait differences between samples

Fisher’s exact test analyses were carried out in order to determine the variation between small samples or between different chronological phases identified in a single archaeological site. In this way, we could estimate whether the analysed samples could be clustered together for further analyses, and also get some more insights in the nature of the most relevant traits indicating biological differences between samples.

This method was applied on the dichotomised (presence/absence values) data. Moreover, in order to eliminate significant results that were due to chance, a Bonferroni correction to the significance level was applied (Goeman & Solari, 2014). This correction consisted on dividing the P value that we considered for at test to be significant (P<0.05) by the number of independent comparisons being made (X); therefore, the corrected new P value would be: 0.05/X.

3.2.2.4. Multivariate methods for the determination of biological affinities: biological distance and Principal Components Analysis

Biological distance calculations are useful in order to calculate the biological affinities between archaeological samples, as well as between extant ones. There are many different distances that can be applied for this purpose based on phenotypic data.

In this work we selected the Mean Measure of Divergence (MMD) (Smith, 1972) which has used by many researchers for long time due to its track record and because it is easy to interpret (Irish, 2010). The formula has evolved in order to compensate for different variances in the weighting of traits and to make the formula reliable for samples with small size (N≥10). The formula applied in this work contained Freeman and Tukey’s angular transformation to correct for low or high trait frequencies and small sample sizes (Harris & Sjvøld, 2004), and was the following:

$$MMD = \frac{\sum_{i=1}^{r} \quad (\theta_{1i} - \theta_{2i})^2 - (1/(n_{1i} + {}^{1}\!/_{2}) \; + 1/(n_{2i} + {}^{1}\!/_{2})}{r}$$

In this formula:

r = number of uncorrelated traits
θ = angular transformation, where the observed proportion, p, is the estimator of the population proportion, P: θ = [1/2] sin $^{-1}$ (1 - (2k)/(n + 1)) + [1/2] sin $^{-1}$ (1-2 (k + 1)/(n + 1))
k = count of positive observations for trait "i"
n = number of individuals examined for trait "i"

In order to determine if two samples are significantly different, the MMD has to be compared to its standard deviation (SD). Therefore, if MMD>2xSD, the null hypothesis of P1=P2 was rejected at the 0.025 confidence level. The SD is obtained from the variance value of the MMD: SD= √Var(MMD). Therefore, the formula to calculate the MMD's variance (Green *et al.*, 1979; Sjøvold, 1973) was expressed as:

$$var(MMD) = \frac{2 \quad \sum_{i=1}^{r} \quad (1/(n_{1i} + {}^{1}\!/_{2}) \; + 1\,(n_{2i} + {}^{1}\!/_{2}))^{\,2}}{r^2}$$

An issue that might happen with the MMD calculation is that when the internal variability of a sample is greater than the one between the two samples being compared, this might result in negative MMD values. These values are statistical artefacts, and therefore, when this case happened the values were set to 0 (Vargiu *et al.*, 2009; Irish, 2010).

The matrixes obtained from the distance values between samples were graphically represented in multi-dimenisonal scaling (MDS) (Kruskal & Wish, 1978) plots with PAST software (Hammer *et al.*, 2001). This method allowed a more intuitive interpretation of the affinities among the analysed samples. The MDS representation is accompanied by indicators of the quality of the same, such as Shepard's plot and stress value. Usually, stress values <0.10 are considered excellent and those ≥0.15 bad or unacceptable (Borgatti, 1997).

In addition to the biological distance calculation and the graphic representation of the obtained distances, Principal Component Analyses (PCA) were carried out to support the results obtained with the previous analyses. This method, although it is not a distance analysis, provided tendencies on the relationships between the analysed samples. Moreover, it also provided information about the weight that each of the analysed variables hds on the distribution observed in the chart, which helped interpreting the results obtained by the MMD and MDS.

Figure 26. Example of ASUDAS plaques for some traits.

4. RESULTS

The objectives of the present dissertation have been covered in the following peer-reviewed publications and works in preparation:

- López-Onaindia D., Otxoa de Amezaga A., Subirà M.E. 2015. **A case of bilateral macrodontia of mandibular second premolars from a Chalcolithic context in the Iberian Peninsula**. Anthropologischer Anzeiger 72: 359-368. ***Objective 1***.

- Subirà M.E., López-Onaindia D., Yll R. 2016. **Cultural Changes in Funeral Rites During the Neolithic in the Northeast of the Iberian Peninsula? The Cave of Pantà de Foix (Barcelona)**. International Journal of Ostearchaeology 26: 104-113. ***Objectives 1 and 2.1***.

- López-Onaindia D., Subirà M.E. 2017. **Prehistoric funerary complexity in northern Iberia studied by using dental morphology**. Homo-Journal of Comparative Human Biology DOI:10.1016/j.jchb.2017.03.002. ***Objective 2.1***.

- López-Onaindia D., Coca M., Gibaja J.F., Subirà M.E. *in press*. **Biological Differences Related to Cultural Variability during the Neolithic in a Micro-Geographical area of the Iberian Peninsula**. Archaeological and Anthropological Sciences. ***Objective 2.1***.

- López-Onaindia D., Schmitt A., Gibaja J.F., Subirà M.E. *Submitted.* **An approach to the Neolithic and Chalcolithic populations around the Pyrenees, where they a natural barrier or a natural passage for human populations?** Trabajos de Prehistoria ***Objective 2.1***.

- López-Onaindia D., Gibaja J.F., Subirà M.E. *submitted.* **Heirs of the glacial maximum: Mesolithic groups along the Iberian Peninsula share the same biological origins**. American Journal of Physical Anthropology. ***Objectives 2.2 and 3***.

- López-Onaindia D., Gibaja J.F., Subirà M.E. *in preparation.* **Dental non-metric variability suggests a dual-model spread, with great influence of hunter-gatherers for the Neolithic in the Iberian Peninsula**. ***Objective 3***.

Non-metric dental analysis of human interactions around the Pyrenees during the Neolithic and their biological impact

Estudio mediante el análisis de caracteres no métricos dentales de las interacciones humanas al rededor de los Pirineos y su impacto biológico durante el Neolítico

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Abstract

Interactions across the Pyreneans during the Middle-Neolithic have been described for a long time. This work analyses the biological affinities of different groups from both sides of the mountains that represent the Populations of the Middle- and Late-Neolithic by means of the dental morphology. Our results suggest that there were differences between populations, both at each side of the Pyrenees and also across them. Nevertheless, the coastal groups across the mountains show more affinities between each other. Therefore, the results indicate that the trade activities registered in the coastal area between both sides of the Pyrenees would have greater biological impacts in the homogenisation of the groups than those for example between the coastal and mountain areas to the south of them.

Resumen

Durante mucho tiempo se han descrito las relaciones y afinidades arqueológicas que se intuían para el periodo del Neolítico Medio a los dos lados de los Pirineos. En este trabajo analizamos, mediante el estudio de la morfología dental, las afinidades biológicas entre grupos del Neolítico Medio y Final de ambos lados de dichas montañas. Los resultados indican la presencia de grupos biológicamente diferentes en cada uno de los lados de los Pirineos, y observamos algunas diferencias entre ambos lados también. Sin embargo, también observamos grandes afinidades entre los grupos más costeros de ambos lados, lo que indicaría que los intercambios costeros tendrían un mayor impacto en la homogenización de las poblaciones que aquellos que ocurrían en la zona de montaña o entre la costa y la montaña.

Key words: Exchange, biological affinities, Chasséen, Sepulcres de Fossa, Solsonian
Palabras clave: Intercambio, afinidades biológicas, Chasséen, Sepulcros de Fossa, Solones

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Introduction

The first Neolithic evidences in the Northwester Mediterranean date from the beginning of the 6th millennium cal BC. The origin of these populations and the process known as Neolithisation has been debated throughout the last decades. These debates have been based on two different points of view for the interpretation of Neolithisation, the autoctonists and diffusionists, in the way to evaluate in combination the last Hunter-Gatherer communities from the Mesolithic and the first Farmers from the Neolithic (Bernabeu, 2006; Binder & Perrin, 2014; Vicent, 1997; Zilhao, 1997). In the case of the Northeast of the Iberian Peninsula there is little information regarding the moment of transition, due to the absence of sites from the end of the 7th and beginnings of the 6th millennium cal BC. This absence of remains might be related to a climatic cooling event around 8,200 BP (Berger & Guilaine, 2008; Morales & Oms, 2012), but new dating essays on Mesolithic materials must confirm this correlation.

Taking into account the archaeological data recovered to date, the Neolithisation in the Northwestern area of the Mediterranean can be linked to two events (García Martínez de Lagrán, 2015). The first of the events, after 5,800 cal BC, is characterised by pottery with *Impressa-Ligur* style decoration (Bernabeu et al. 2011; Oms, 2014). These first Neolithic evidences are scarce, and related to an economy based on agriculture and livestock, dominated by herds of goats (*Capra hircus*) and emmer wheat (*Triticum disccocum*) crops. These archaeological sites are localised in zones near the Mediterranean sea; both in Southeast France, represented by the cases of Peito Signado and Pont de Roque-Haute (Guilaine et al. 2017; Briois & Manen, 2009), and in the East of the Iberian Peninsula with the sites of Guixeres de Vilobí and El Barranquet (Bernabéu et al. 2011; Oms et al. 2014).

The second event was related to the presence of Cardial decoration in the pottery, and is documented after 5,600-5,500 cal BC (Guilaine et al. 2007; Oms et al. 2016). The sites that represent this moment are also found near the coastal and pre-coastal areas of the Northwest

Mediterranean, and in isolated cases also in inland areas. At this time the economy was dominated by the culture of naked wheat (Triticum aestivun/durum) and barley (Hordeum vulgare), and by herds of ovicaprids (Ovis and Capra) (Saña, 2013), while the bovine and swine domestication was still of little importance.

Up until now, the quantity of burials discovered in the Iberian Peninsula between the middle of the 6th and the middle of the 5th Millennium cal. BC has been fairly anecdotal (Bosch and Tarrús 1991; Blasco et al. 2005; Gonzalez et al. 2011; Oms et al. 2017). Nevertheless, this situation changes towards the second half of the 5th Millennium cal BC. It was then when a proliferation of funerary evidence becomes available, either in the form of necropolises or as isolated burials in different areas of Northwestern Mediterranean, and concretely in the Northeast of the Peninsula (Martín 2009, Gibaja y Clop, 2012, Gibaja et al. 2016 a).

As regards to the funerary structures, between the end of the 5th and a long period during the 4th millennium cal BC, two large groups can be identified in the Northeast of the Iberian Peninsula: burial pits dug in the soil, and sepulchres made of stone cists. The pit structures are usually found in areas near the coast, while the cists are found in the inland and Pyreneans. These two groups equally exhibit certain variations concerning their morphology, size, and the employed constructive elements (Martin et al. in press). At the same time, some of the burials were not made *ex profeso*, but by re-using different kinds of structures; we refer to the re-use of silos in which the wastes include one or several individuals or the re-use of mines as burial places, which is the case of the Prehistoric Mines of Can Tintorer/Gavà (Bosch and Borrell 2009; Villalba 1999). These kind of funerary structures are also found in southern France, in the cultural ensemble known as Chasséen, which mainly comprises the Midi-Pyrénées, Languedoc and Provence areas.

Usually, these burials contain a single individual: man, woman, or child. Only sporadically, there are structures enclosing three or more individuals. Bodies are usually deposited in supine *de cubitus* with folded legs and arms in variable positions. Occasionally bodies are found fully stretched or in *de cubitus*. However, certain graves exhibit bodies with no anatomical connection, or displaying only a partial connection, while on particular occasions, individuals have been identified displaced towards the sides of the tomb to make room for those buried later. Recent studies on funeral taphonomy have provided important information about certain aspects that had not been treated so far. Thus, for example, today we know that these individuals were not simply deposited in the bottom of the funerary structure, but occasionally placed in the interior of the tomb within rigid boxes, probably wooden, or in bags (Allièse et al. 2014).

During this period there are evidences of exchange networks at different levels that connect both sides of the Pyrenees, which according to the evidence is stronger on a East-to-West direction than in the opposite sense (Gibaja *et al.* 2016 b; Terradas *et al.* 2016). In this context, in the sepulchres from the Northeast of the Iberian peninsula researchers have found imported materials such as Barrémo-Bédoulian Flint from Vaucluse (Provence) (Binder, 1998; Briois, 2005; Gassin *et al.* 2011; Gibaja *et al.* 2013; Léa, 2004), polished axes originated in the Alps (Léa, 2005; Pétrequin *et al.* 2012; Vaquer *et al.* 2011), and Obsidian blades and nuclei from Sardinia (Gibaja *et al.* 2013; Terradas *et al.* 2014). On the other hand, pieces made from Variscite exploited at Can Tintorer mines from Gava (Barcelona) appeared in Chasséen sites to the west of the Rhone (Terradas *et al.* 2016).

The analyses on raw material, funerary culture, techniques and chronology suggest that there were similar cultural backgrounds and intense trade interactions at both sides of the Pyrenees. Nevertheless in order to determine whether these similarities were due to cultural influences or there was a common biological origin for the human groups it is necessary to analyse their biological affinities. One of the most reliable methodologies to analyse these relationships between samples is dental morphology, which have been applied in several contexts in the last decades (Coppa *et al.* 2007; Desideri, 2011; Irish, 2006; Irish *et al.*2017; López-Onaindia & Subirà, 2017; López-Onaindia *et al.* in press) and has been proved that it provides results that correspond with those obtained by analysing Nuclear DNA (Hubbard *et al.*2015). Furthermore, due to the hardness of the enamel, teeth are usually the best-preserved osteological materials in the funerary contexts from this region and period.

Therefore, the aim of this work is to determine the biological relationships between Middle and Late Neolithic groups from both sites of the Pyreneans that represent all the funerary cultures observed in each area.

Materials and methods

In this work we include dental morphological data from 32 Neolithic and Chalcolithic sites from the Northwest of the Mediterranean (Figure 1). Data from the sites located in the Iberian Peninsula (20 sites, including 255 individuals and their 3,661 teeth) that have already been published are analysed (López-Onaindia & Subirà, 2017; López-Onaindia *et al.* in press; Pascual *et al.* 2016; Subirà *et al.* 2016). In addition, the samples from southern France include published data from Le Crès site (Schmitt, 2008), and data from new 3,977 human teeth from 11 archaeological sites studied for this work (Table 1).

The French samples belong both to the Middle- and Late-Neolithic, and almost the full extension (West-to-East) of the Southern part of the country. At the same time, the Middle-Neolithic samples are grouped in three ensembles regarding their geographical and cultural characteristics: Middle-Neolithic from Languedoc-Midi Pyrénées; Middle-Neolithic from Provence; and Montbolò Neolithic.

The Middle-Neolithic from Languedoc-Midi Pyrénées is formed by the samples from, La Terrasse, /La Vimona, Zac Agora, Narbons, Saint Gely-du-Fesc, et Le Crès. The former site is formed by hundreds of pits in the area of Tolouse, of which 20 were burials (Gandelin & Vaquer, 2008; Marlière *et al.* 2008). On regards to Narbons, this site is located to the southeast of Montesquieu-de-Lauragais (Haute-Garonne) and provided six pit structures at the time of the archaeological intervention (Tchérémissinof *et al.* 2005). Four of these structures resulted to be sepulchres. Three are attributed to the Chaseen culture, and number 1020 is situated at the end of Middle Neolithic. The interventions in Saint Gely du Fesc were hold in 1996 (Hérault), provided four burial pits in a concentred area of less than 25m^2, each of them containing a single individual (Vignaud *et al.* 1997). Unpublished radiocarbon dates on each subject indicate that three belonged to the end of Middle Neolithic and one to the beginning of Middle Neolithic (« Neolithique moyen I » according to the french chronological system for the south of France). Finally Le Crès site (Hérault) provided 190 negative structures, of which 31 were burials that were excavated during 2000 and 2001 (Loison *et al.* 2004 ; Loison et Schmitt, 2009). 30 of these pits correspond to Chaseen burials and contained 49 individuals from this period. Moreover, compared to other sites this represented a wide variety of tomb typologies, from simple pits to proto-megalithic structures.

In the case of the Middle-Neolithic from Provence, the group includes the samples from Clos de Roque Les Clavelles, Les Martins and Le Collet Redon. This last site is the sole collective burial of this group, located in La Couronne (Schmitt *et al.* in press b); the radiocarbon dates give a chronological interval situated between Middle and Late Neolithic. The burial provided a minimum number of 11 individuals in primary and secondary deposits. The tomb is installed in a quadrangular feature measuring 2.4 x 2.2 m. The walls of the pit are built with piled up stones. Les Martins is a site excavated in 1986 that produced two Middle-Neolithic burials (St. 6 and St. 8), consisting on individual burials in pits with a child and an adult male (d'Anna *1993*; Van Willigen et al. 2014). In the case of Clos de Roque, 6 pits containing individual burials where discovered in 2011 (Remicourt *et al.* 2014; Schmitt *et al.* in press a). From these six individuals, four belong to the beginning of the Middle-Neolithic (called “Neolithique moyen I” (St. 2209, 2215; 2205, 2224).

Les Clavelles is an unpublished site. It provided a circular pit composed of two layers. 5 individuals were buried in this feature. An unpublished radiocarbon date on human bone indicate its belonging to the end of the V millennium. The hypogeum of “les Crottes” was excavated in 1966. It is composed of 5 layers. Two of them are funerary collective deposits, level 2 and 5 (Courtin, 1974; Sauzade, 1983). The latest dates from the last quarter of the Vth millennium.

The remains from the caves of Bélesta and Montou form the Montbolò group, in the Roussillon area. La Caune de Bélesta was excavated in 1983, when remains of a collective burial were identified together with many pieces of pottery (Claustre *et al.* 1993) that are attributed to the Montbolò culture. Montou is located in Corbères-les-Cabanes (Eastern Pyrenees), and it represents a collective burial like Bélesta (Claustre & Ponsich, 2000; Valentin *et al.* 2003).

The last site analysed for the work is Grôtte Mykolas cave which was excavated in 2007 (Chancerel *et al.* 2007). This site is located to the North of Bugue (Aquitania) and its chronological affiliation corresponds to the Late-Neolithic age. According to the initial report an NMI of 9 individuals was calculated, but dental remains indicate that there were at least 12 inhumated individuals.

The analysis of the teeth was carried out following the Arizona State University's Dental Anthropology System (ASUDAS) (Turner *et al.* 1991), which considers 35 non-metric dental traits. In individuals with full dentition, these 35 traits provide 121 variables for individual. Most traits are not just present or absent, but ranked in a scale of expression, and the level at which they are represented in each of the antimers of an individual may vary. For this reason, the antimere showing the highest level of expression, which is believed to be the one representing the trait's maximum potential for the individual and be genetically more reliable, is selected in each individual (Turner, 1985; Turner *et al.* 1991).

In order to identify correlations between traits, Kendall's Tau-b analysis was done on the ranked data (Irish, 2010) with IBM SPSS 20.00. A correlation was considered strong when the Tau-b value is superior to 0.5, and for it to be statistically significant we considered that the N must be >10 and the p value <0.05. This step is necessary to edit the database before calculating the biological distances, as one of the traits of the correlated pair was eliminated in order to avoid differential weighting of the underlying dimensions that might yield erroneous results (Irish, 2010, Sjøvold, 1977).

The ranked ASUDAS values were later dichotomised into presence or absence values, based on their reported morphological thresholds (Nichols, 1989) and according to standard procedure (Turner, 1985; 1987). From these dichotomised data, frequencies for the expression of traits were calculated for the different samples and groups.

Together with one of each pair of correlated traits, those traits that presented no frequency differences in the various samples were excluded from further analysis, because they were non-informative. Due to different conservation state and sample size of the collections included in this work, it was necessary to make different analysis including different variables and samples at different times. The Mean Measure of Divergence (MMD) (Smith, 1972) was calculated between samples as an among-samples phenetic dissimilarity measure. The formula used to calculate the MMD contains Freeman and Tukey's angular transformation to correct for low or high trait frequencies and small sample sizes (Harris & Sjøvold, 2004). Nevertheless, each trait used must have been scored at least 10 times (including present and absent) in each sample. In order to determine if two samples are significantly different, the MMD has to be compared to its standard deviation (SD). Therefore, if MMD>2xSD, the null hypothesis of P1=P2 is rejected at the 0.025 level. In some cases, when the internal variability of a sample resulted greater to that between the two samples compared negative MMD values might result. These values are statistical artefacts, and therefore, they were set to 0 (Vargiu et al.2009; Irish, 2010).

The matrixes obtained with the MMD calculation were graphically represented in Multi-Dimensional Scaling (MDS) (Kruskal & Wish, 1978) using PAST software (Hammer *et al.* 2001). This representation is useful to obtain further information beyond if two samples are significantly different or not. The representations offer a stress value that indicates the accuracy with which the matrix has been represented. Usually, stress values <0.10 are considered excellent, and ≥0.15 unacceptable (Borgatti, 1997). Moreover, Principal Component Analysis (PCA) were carried out with PAST too based on the same traits used to calculate the MMD. These analyses usually provide complementary information on which traits are more involved in the distribution observed on the MDS representation.

Two different sets of MMD calculations were carried out: one that included all the French and Iberian samples except for the Montbolò group, and was based on 10 traits; the other excluded some more French and Iberian samples and included Italian samples (Coppa *et al.* 2007) in order to get a broader context on the relationships observed with the previous analysis.

The Montbolò samples were especially small, and after trait editing to avoid the non-informative and correlated variables, very few variables could be included in MMD calculation. For this reason this samples was compared with Fisher's exact test, for all those traits scoring more than

5 observations, to the Iberian and French samples in order to see which groups present less differences with it.

Results

The number of times a trait was scored in each group, the frequency for the presence of the traits and dichotomic breaking-point for each of them are shown in Table 2.

Some traits provided significant correlation values when analysed with Kendal’s Tau-b. These traits were: *UM2 cusp5* was correlated to UP4 m&d cusps (Tau-b=0.716, N=25) and UM3 cusp5 (Tau-b=0.642, N=19); on the other hand UM1 Metacone and UM3 Carabelli's tubercle were also correlated (Tau-b= 0.725, N=12).

The MMD analysis based on 10 variables that included both French and Iberian samples (Table 3), showed a complex scenario with significant differences among samples from the same side of the Pyrenees, while there are not differences between some of the samples across the mountains. Those samples presenting significant differences at the 0.025 level are the Languedoc-Midi Pyrenees group and the Late Neolithic Mediterranean groups (Roaix, Cova del Pantà de Foix and Can Sadurní). On the other hand, those samples that presented no differences with any other sample were the Middle-Neolithic sample from Provence and Grôtte Mykolas.

When this matrix was represented (Figure 2) we obtained a MDS plot that provided a grouping of samples to the right end of the horizontal axis where two sites from the Iberian Peninsula with pit burials were registered (Los Cascajos, Early- and Middle-Neolithic from Navarre, and Bòbila Madurell) and a Chalcolithic cave from the Mediterranean coast of the same area (Cova del Pantà de Foix). On the other extreme we observe the Middle-Neolithic sample from Languedoc and Midi-Pyrénées area, and the rest of the samples appear in the centre between them.

The PCA analysis for the same traits provides a similar representation to the MDS with the two first components (83.5% of the total variance explained): the Languedoc/Midi-Pyrénées sample was the most divergent from the rest, which was determined by higher frequencies of *LM1 cusp6* and *LM2 cusp 7* (Table 4). On the opposite side the Middle-Neolithic samples from Provence, Bòbila Madurell and Cascajos together with Cova del Pantà de Foix were characterised for having high frequencies for *LP4 cusp number* and relatively high presences of *Hypocone* in both UM1 and UM2.

If we excluded the smallest samples from the analysis (Grôtte Mykolas, Middle-Neolithic from Provence, and Cova del Pantà de Foix) and compare the other samples to Italian samples using 8 traits we obtained the matrix shown in Table 5. With the distance data we observed that Italian samples significantly differed from all Iberian and French samples. In the same sense, the samples from the last two areas differed between each other too; although, in many cases, these distance values were smaller than those that both groups presented respect to the Italians.

The MDS representation of this matrix (Figure 3) shows the Italian Upper-Palaeolithic and Mesolithic sample appeared separated from all the other samples and the Italian Neolithic sample stand in the centre of the plot, while in the other corner French and Iberian samples appeared separated as well. From the Iberian and French samples those showing more affinities to the Italian Neolithic were Cascajos (Early- and Middle-Neolithic from Navarre), Bòbila Madurell (Middle-Neolithic from Catalonia) and Roaix (Late-Neolithic from Provence), while the Langedoc and Solsonian samples appeared farther.

When correlations between the main components in the PCA analysis and the variables were analysed (Table 6), we observed that the Italian groups present UM2 cusp5 and UM1 Carabelli's tubercle in higher frequencies than Iberian and French groups, while the latter had overall more presence of *UI2 shovelling*, this differentiation occurs in the first component. The second component split the French and Iberian samples, not in the same manner as the MDS, but Languedoc and Solsonian Middle-Neolithic groups on one side and the other groups (Middle- and Late-Neolithic samples) on the other corner. In this sense, the most significant trait was the presence of *multiple lingual cusps in LP4*, which was most common in Late-Neolithic samples and the Middle-Neolithic samples of Bòbila Madurell and Los Cascajos.

The Montbolò sample did not show differences for many of the 18 analysed traits with the rest of samples when this was analysed by Fisher's exact test (Table 7). Moreover, when Bonferroni's correction was applied to the significance level ($p<0.0002777$), this sample only differed significantly in one trait from Los Cascajos sample: *LM1 Cusp5*.

Discussion

Although there are many cultural similarities between the two main Middle-Neolithic cultures from Catalonia and Mediterranean France (Sepulcres de Fossa Culture and Chasseen), our results indicate that in the biological background of the different human groups there is some variance. This variance, thought, is not a simple divergence between French and Iberian samples. As it has previously been mentioned, many studies support a dual dispersion model for the Neolithic in the Northeastern area from the Mediterranean (Guilaine, 2003; Cruz-Berrocal, 2013).

In their recent work, Molist and collaborators (2016) analyse different material evidence between the Chasséen and the Sepulcres de Fossa cultures. This study suggests that although the affinities and the common elements between both cultures, each of them has singular elements related to the previous background in the territories. Nevertheless, they do also observe that the similarities between the two groups are greater than that each of them has with any surrounding area. Moreover, both share common characteristics that can be interpreted as heritage from the

Montbolò and Molinot cultures that spread through the eastern Pyrenees. Finally, as it has previously been mentioned, according to many evidence pieces, the exchange networks between these groups at both sides of the Pyrenees were strongly rooted (Gibaja *et al.* 2013; Molist *et al.* 2016; Terradas *et al.* 2014; 2016)

Ancient DNA (aDNA) analyses carried out in Neolithic samples from the Iberian Peninsula show different scenarios depending on which samples are analysed: some show that the Neolithic samples have signals similar to those from Eastern Mediterranean and LBK culture (Olalde *et al.* 2015), while other studies show mixed signals in the different areas of the Iberian Peninsula (de la Rúa *et al.* 2015; Szécsény-Nagy *et al.* 2017). Therefore, a mixed model would be the most accurate one explaining the current evidences. In this sense, some of our previous results evidence slight biological differences between some Iberian samples (López-Onaindia & Subirà, 2017; López-Onaindia *et al.* in press). These works show that in the Northeast of the Iberian Peninsula there was biological variability during the Neolithic, as aDNA works point out. In these cases the samples that significantly diverged from the rest were the Megalithic groups from the Atlantic coast and the Solsonian (stone cist burials) group. Meanwhile, our first approaches in order to shed some light onto the relationship between Iberian Hunter Gatherers and first Farmers analysing dental morphology suggested that there were not significant differences between them (López-Onaindia *et al.* submitted).

The present results show that, overall, those groups from coastal areas or valleys near the coast present differences with fewer groups than non-coastal samples, both in each region and between regions. Some parts of the exchange must have used coastal routes, such as maritime connection with Sardinia that was the base of the obsidian diffusion. It might also be plausible that the most intense route for the networks between Southern France and Northern Iberian Peninsula would happen in near the coast. Therefore, these populations would have more diverse biological backgrounds than those from inner land. The sample from Los Cascajos, although it is in the inland, shows affinities similar to those from the Catalonian coast samples. In this case, aDNA analyses have shown that it is a sample with high genetic variability and would not be an isolated group (Hervella *et al.* 2016).

Moreover, all French and Iberian samples significantly diverge from the Italian groups. However, these differences are smaller with the Neolithic than with the Hunter-Gatherer sample. Concretely, the Languedoc-Midi Pyrenees and Solsonian samples are the most divergent from the Italian Neolithic one, while Bòbila Madurell (Vallès area) and Los Cascajos present slighter differences with it. Hence, it is plausible that some migration from the East arrived into French and Iberian territory with the spread of the agriculture, but that seems to have been less intense than that observed in the Italian Peninsula (Coppa *et al.* 2007). Furthermore, the Italian Palaeolithic-Mesolithic sample diverges significantly from the Iberian one (López-Onaindia *et al.* submitted), which would result on different previous biologic backgrounds in each area.

Finally, it must also be mentioned that in those two Middle-Neolithic groups that diverge most from the rest, Solsonian area and Languedoc-Midi Pyrenees, there are representations of burials done in stone slab cists, while in the other areas these are not present. In the case of the Late-Neolithic, these samples are also diverse, but show similar affinities with most Middle-Neolithic samples. This is a trend that it has been previously observed in our works, as groups get more uniform between them towards Bronze Age (López-Onaindia & Subirà, 2017; López-Onaindia *et al.* in press).

In summary, our results are compatible with a dual pattern model for the dispersion of the Neolithic in the Northwest of the Mediterranean, although the impact of incoming eastern farmers would not be as important as in other areas of the Mediterranean. In addition, we observe that this effect is similar in the Iberian Peninsula and France, and that the affinities that are observed in material culture between the Chasséen and Sepulcres de Fossa culture have a parallel in biological means. Lastly, the similarities between inhabitants from coastal areas are greater, as probably these were more open to external influences related to exchange networks; moreover, the inner groups also present some variation in funerary culture with the presence of burials in cists.

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Figure 1. Map showing the location of the samples included in this work. 1, Grôtte Mykolas; 2, La Terrasse, Villeneuve-Tolosane/La Vimona et Zac Agora, Cugnaux; 3, Narbons; 4, Le Crés; 5, Saint Gely du Fesc, Rouergas; 6, Les Martins, Roussillon; 7, Les Clavelles Lurs; 8, Collet Redon, Martigues; 9, Clos de Roque, Saint-Maximin; 10, Hypogée des Crottes, Roaix; 11, La Caune de Bélesta; 12, Montou; 13, Los Cascajos; 14, Middle-Neolithic Solsonés; 15, Bòbila Madurell; 16, Can Sadurní; 17, Cova del Pantà de Foix.

Figure 2. MDS representation of the distance matrix obtained for Iberian and French samples based on 10 traits. The stress value associated to the representation is 0.14. Abbreviations: GrôtteMyk: Grôtte Mykolas; Cascajos: Los Cascajos; BobM: Bòbila Madurell; CPF: Cova del Pantà de Foix.

Figure 3. MDS representation of the distance matrix obtained for the samples analysed for this work and compared to the Italian series. This matrix was obtained comparing 8 traits, and the stress value of the representation is 0.10. Abbreviations: Cascajos: Los Cascajos; BobM: Bòbila Madurell; UPMit: Upper Palaeolithic and Mesolithic Italy; NEOit: Neolithic Italy.

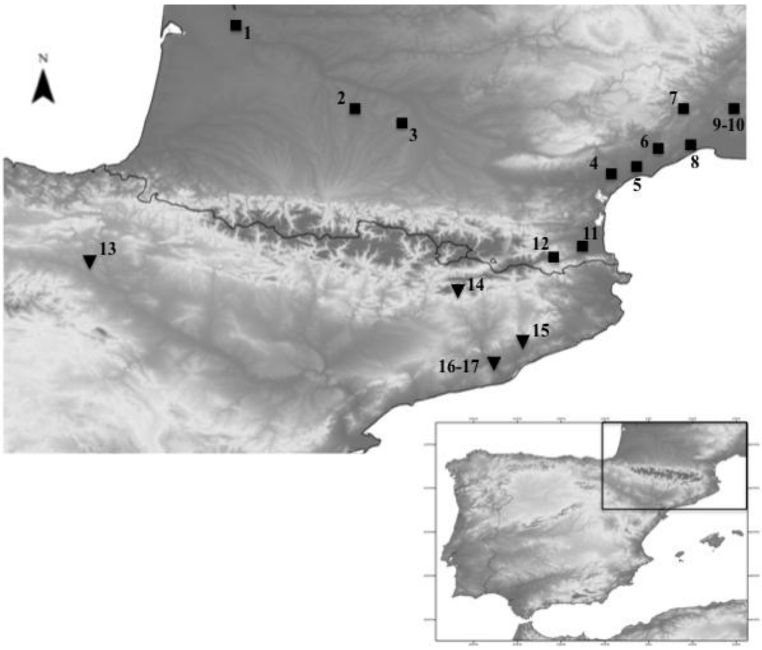

Fig. 1

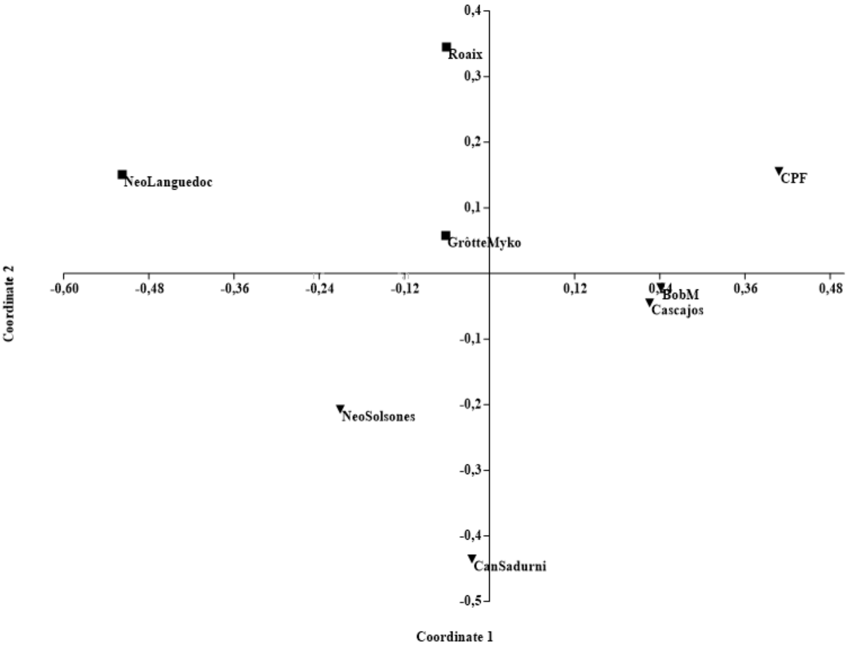
Roaix
NeoLanguedoc
CPF
GrötteMyko
BobM
Cascajos
NeoSolsones
CanSadurni
0,4
0,3
0,2
0,1
-0,1
-0,2
-0,3
-0,4
-0,5
-0,60
-0,48
-0,36
-0,24
-0,12
0,12
0,24
0,36
0,48
Coordinate 2
Coordinate 1

Fig. 2

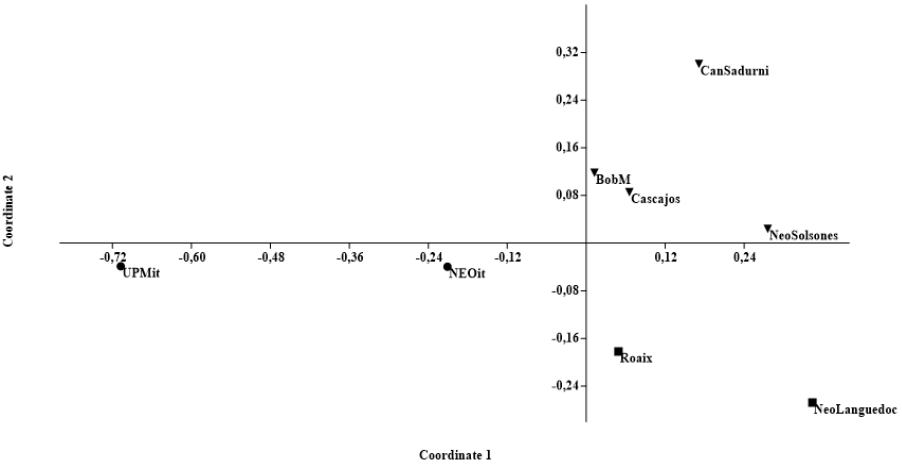
CanSadurni
BobM
Cascajos
NeoSolsones
UPMit
NEOit
Roaix
NeoLanguedoc
0,32
0,24
0,16
0,08
-0,08
-0,16
-0,24
-0,72
-0,60
-0,48
-0,36
-0,24
-0,12
0,12
0,24
Coordinate 2
Coordinate 1

Fig. 3

Table 1. Summary of the novel samples analysed for this study, indicating the chronology they belong to, geographical area and sample size information

Name	Chronology	Geographical area	References	NMI	Number of teeth
Grôtte Mykolas, Bugue	Late Neolithic	Aquitania	Chancerel *et al*.2007	12	256
La Terrasse, Villeneuve-Tolosane/La Vimona et Zac Agora, Cugnaux	Middle Neolithic	Midi-Pyrenees/Languedoc	Gandelin & Vaquer 2008	10	183
Narbons, Montesquieu de Lauragais	Middle Neolithic	Midi-Pyrenees/Languedoc	Tchérémissinof *et al*. 2005	3	71
Saint Gely du Fesc, Rouergas	End of middle Neolithic	Languedoc-Rousillon	Vignaud *et al*. 1997	4	11
Les Martins, Roussillon	Middle Neolithic	Provence	d'Anna *et al*. *1993*	2	40
Les Clavelles Lurs	Middle Neolithic	Provence	Inedited	4	36
Collet Redon, Martigues	End of middle Neolithic	Provence	Schmitt *et al*. in press b	6	116
Clos de Roque, Saint-Maximin	Beginning of middle Neolithic	Provence	Remicourt *et al*. 2014; Schmitt *et al*. in press a	3	73
Hypogée des Crottes, Roaix	Late Neolithic	Provence	Courtin, 1974; Sauzade, 1983	159	2,994
Caune de Belesta, Bèlesta	Early- Middle-Neolithic	Rousillon	Claustre *et al*. 1993	10	54
Montou, Corbère-les-Cabanes,	Early- Middle-Neolithic	Rousillon	Claustre & Ponsich, 2000; Valentin *et al*.2003	8	143
				221	3,977

Table 2.1. Sample sizes, presence recount, frequencies, and dichotomic breaking points for the studied maxillary traits. The traits in bold were used for the analysis between Iberian and French samples; those in italics were the ones used for the comparison with the Italian series.

		Grôtte Mykolas			Neò Moyen Midi Pyrenées-Languedoc			Neò Moyen Provence			Roaix			Belesta & Montou		
Trait	**Breaking point**	N	Presence	Freq.	N	Presence	Freq	N	Presence	Freq.	N	Presence	Freq.	N	Presence	Freq.
I1 Interruption Groove	1/0-1	8	1	0.125	27	6	0.222222	9	0	0	115	13	0.11304	9	0	0
I1 Shovel	3-6/0-6	4	0	0	25	11	0.44	3	0	0	67	7	0.10448	5	0	0
I1 Double shovel	2-6/0-6	6	0	0	26	0	0	8	0	0	106	4	0.03774	8	0	0
I1 tuberculum dentale	2-6/0-6	4	1	0.25	26	5	0.192308	4	0	0	50	14	0.28	3	0	0
I2 Interruption Groove	1/0-1	9	1	0.11111	30	7	0.233333	11	1	0.09091	113	17	0.15044	8	3	0.375
I2 Shovel	*3-7/0-7*	7	2	0.28571	*25*	*13*	*0.52*	9	1	0.11111	*75*	*34*	*0.4533*	3	1	0.33333
I2 Double Shovel	2-6/0-6	9	0	0	23	1	0.043478	9	0	0	108	3	0.02778	7	0	0
I2 tuberculum dentale	2-6/0-6	5	2	0.4	25	6	0.24	6	0	0	52	9	0.17308	4	2	0.5
I2 Root	1/1-2	7	7	1	2	2	1	5	5	1	95	95	1	1	1	1
I2 peg shape	2/0-2	8	0	0	4	0	0	11	0	0	107	0	0	7	0	0
I2 Congenital absence	1/0-1	10	0	0	7	0	0	11	0	0	14	1	0.07143	7	0	0
C tuberculum dentale	2-6/0-6	4	1	0.25	25	6	0.24	6	1	0.16667	65	22	0.33846	2	0	0
C Mesial ridge	2-5/0-5	3	0	0	18	0	0	4	0	0	71	0	0	2	0	0
C Distal accessory ridge	2-5/0-5	2	1	0.5	18	2	0.111111	5	2	0.4	66	30	0.45455	2	1	0.5
C Root	1/1-2	14	14	1	0	0		5	5	1	109	109	1	2	2	1
P3 m&d cusps	1/0-1	7	0	0	1	0	0	9	0	0	77	0	0	4	0	0
P3 enamel ext.	1-3/0-3	12	0	0	3	0	0	7	1	0.14286	90	3	0.03333	5	0	0
P3 Root	1/1-2	7	5	0.71429	17	10	0.588235	6	3	0.5	59	27	0.45763	2	1	0.5
P4 m&d cusps	1/0-1	6	0	0	3	0	0	11	0	0	119	2	0.01681	2	0	0
P4 enamel ext.	1-3/0-3	10	0	0	1	0	0	9	0	0	146	1	0.00685	5	0	0
P4 Root	1/1-2	6	6	1	11	10	0.909091	7	7	1	108	108	1	2	2	1
M1 Metacone	2-5/0-5	14	14	1	7	7	1	15	15	1	105	105	1	13	13	1
M1 Hypocone	**2-5/0-5**	**14**	**14**	**1**	**39**	**38**	**0.9744**	**15**	**15**	**1**	**101**	**101**	**1**	13	13	1
M1 Cusp 5	1-5/0-5	8	0	0	2	0	0	14	0	0	90	1	0.01111	9	1	0.11111
M1 Carabelli	*2-7/0-7*	1	0	0	*36*	*4*	*0.11111*	8	4	0.5	*49*	*23*	*0.4694*	8	3	0.375
M1 C2 parastyle	*1-5/0-5*	10	0	0	*38*	*0*	*0*	11	0	0	*87*	*0*	*0*	9	0	0
M1 Enamel ext.	1-3/0-3	13	0	0	35	2	0.057143	11	2	0.18182	81	6	0.07407	10	1	0.1
M1 Root	3/1-3	11	11	1	3	3	1	8	7	0.875	46	44	0.95652	3	2	0.66667
M2 Metacone	**2-5/0-5**	**14**	**14**	**1**	**10**	**10**	**1**	**12**	**12**	**1**	**119**	**118**	**0.992**	9	9	1
M2 Hypocone	**2-5/0-5**	**14**	**11**	**0.786**	**31**	**22**	**0.7097**	**12**	**9**	**0.75**	**107**	**74**	**0.692**	9	4	0.44444
M2 Cusp 5	***1-5/0-5***	**13**	**0**	**0**	***24***	***3***	***0.125***	**12**	**1**	**0.083**	***101***	***10***	***0.1***	8	4	0.5
M2 Carabelli	2-7/0-7	9	0	0	25	1	0.04	10	1	0.1	60	3	0.05	3	0	0
M2 C2 parastyle	**1-5/0-5**	**14**	**0**	**0**	**32**	**0**	**0**	**11**	**0**	**0**	**105**	**3**	**0.029**	6	0	0
M2 Enamel ext.	1-3/0-3	12	1	0.08333	30	1	0.033333	8	0	0	92	5	0.05435	7	0	0
M2 Root	3/1-3	9	6	0.66667	4	2	0.5	5	2	0.4	63	48	0.7619	1	1	1
M3 Metacone	2-5/0-5	11	11	1	7	7	1	7	7	1	92	88	0.95652	4	4	1
M3 Hypocone	2-5/0-5	11	5	0.45455	7	0	0	7	1	0.14286	89	42	0.47191	4	1	0.25
M3 Cusp 5	1-5/0-5	11	6	0.54545	6	1	0.166667	7	5	0.71429	88	36	0.40909	4	1	0.25
M3 Carabelli	2-7/0-7	8	0	0	2	0	0	7	1	0.14286	63	0	0	2	0	0
M3 C2 parastyle	1-5/0-5	10	2	0.2	7	0	0	7	0	0	87	2	0.02299	4	0	0
M3 Enamel ext.	1-3/0-3	10	1	0.1	8	1	0.125	6	0	0	72	6	0.08333	4	0	0
M3 Root	2/0-2	10	3	0.3	5	0	0	2	0	0	43	6	0.13953	1	0	0
M3 (<7)/reduce	1/0-1	9	0	0	7	0	0	7	0	0	87	1	0.01149	2	0	0

Table 2.2. Sample sizes, presence recount, frequencies, and dichotomic breaking points for the mandibular traits studied. The traits in bold were used for the analysis between Iberian and French samples; those in italics were the ones used for the comparison with the Italian series.

		Grôtte Mykolas			Neò Moyen Midi Pyrenées-Languedoc			Neò Moyen Provence			Roaix			Belesta & Montou		
Trait	**Breaking point**	N	Presence	Freq.	N	Presence	Freq	N	Presence	Freq.	N	Presence	Freq.	N	Presence	Freq.
I1 Shovel	2-3/0-3	8	0	0	22	0	0	6	0	0	90	0	0	2	0	0
I2 Shovel	*2-3/0-3*	14	0	0	*28*	*0*	*0*	9	0	0	*89*	*4*	*0.0449*	6	0	0
C Distal accessory ridge	2-5/0-5	4	1	0.25	14	1	0.071429	1	0	0	61	5	0.08197	3	2	0.66667
C Root	1/1-2	10	10	1	20	16	0.8	4	2	0.5	61	61	1	3	3	1
P3 Lingual cusps	2-9/0-9	16	1	0.0625	28	6	0.214286	6	1	0.16667	148	35	0.23649	4	1	0.25
P3 Enamel ext.	1/0-1	18	0	0	6	0	0	7	1	0.14286	173	0	0	4	0	0
P3 Root	1/1-2	15	15	1	16	15	0.9375	3	3	1	128	127	0.99219	1	1	1
P4 Lingual cusps	***2-9/0-9***	**13**	**8**	**0.615**	***17***	***4***	***0.2353***	**10**	**7**	**0.7**	***117***	***77***	***0.66***	4	2	0.5
P4 Enamel ext.	1/0-1	17	0	0	7	0	0	6	0	0	133	0	0	6	0	0
P4 Root	1/1-2	12	12	1	2	2	1	3	3	1	98	98	1	3	3	1
M1 Groove pattern	Y/Y,+,X	6	4	0.66667	4	4	1	2	2	1	89	77	0.86517	8	8	1
M1 Cusp nº	6-7/4-7	12	0	0	4	0	0	11	0	0	127	6	0.04724	10	0	0
M1 Defflecting wrinkle	2-3/0-3	0	0		2	0	0	1	0	0	14	0	0	6	1	0.16667
M1 Distal crest	1/0-1	3	0	0	2	0	0	4	0	0	45	0	0	7	0	0
M1 Protostylid	2-7/0-7	7	0	0	2	0	0	5	0	0	73	0	0	6	0	0
M1 Cusp 5	***3-5/0-5***	**12**	**11**	**0.917**	***28***	***26***	***0.9286***	**11**	**7**	**0.636**	***128***	***112***	***0.88***	10	8	0.8
M1 Cusp 6	**2-5/0-5**	**12**	**0**	**0**	**26**	**1**	**0.0385**	**11**	**0**	**0**	**125**	**1**	**0.008**	10	0	0
M1 Cusp 7	***1-4/0-4***	**12**	**0**	**0**	***28***	***3***	***0.1071***	**11**	**0**	**0**	***130***	***1***	***0.01***	12	0	0
M1 Enamel ext	1-3/0-3	15	1	0.06667	7	0	0	9	1	0.11111	117	4	0.03419	8	1	0.125
M1 Root	3/1-3	12	0	0	18	0	0	7	0	0	70	1	0.01429	5	0	0
M2 Groove pattern	Y/Y,+,X	7	0	0	21	2	0.095238	3	0	0	121	11	0.09091	5	0	0
M2 Cusp nº	4/4-6	12	12	1	6	6	1	10	6	0.6	165	135	0.81818	6	6	1
M2 Defflecting wrinkle	2-3/0-3	1	0	0	0	0		3	0	0	19	0	0	1	0	0
M2 Distal crest	1/0-1	6	0	0	0	0		7	0	0	108	0	0	4	0	0
M2 Protostylid	2-7/0-7	5	0	0	1	0	0	10	0	0	102	1	0.0098	5	0	0
M2 Cusp 5	3-5/0-5	12	0	0	28	4	0.142857	10	3	0.3	161	5	0.03106	6	0	0
M2 Cusp 6	3-5/0-5	12	0	0	6	0	0	10	0	0	163	1	0.00613	6	0	0
M2 Cusp 7	**1-4/0-4**	**12**	**0**	**0**	**28**	**3**	**0.1071**	**10**	**0**	**0**	**164**	**1**	**0.006**	6	0	0
M2 Enamel ext	1-3/0-3	13	2	0.15385	8	0	0	9	1	0.11111	139	10	0.07194	6	1	0.16667
M2 Root	1/1-3	9	1	0.11111	2	1	0.5	7	1	0.14286	76	15	0.19737	2	0	0
M3 Groove pattern	Y/Y,+,X	10	3	0.3	4	1	0.25	2	0	0	78	11	0.14103	3	1	0.33333
M3 Cusp nº	4/4-6	10	2	0.2	8	5	0.625	7	4	0.57143	88	36	0.40909	5	5	1
M3 Defflecting wrinkle	2-3/0-3	1	0	0	0	0		3	1	0.33333	17	1	0.05882	0	0	
M3 Distal crest	1/0-1	7	1	0.14286	3	0	0	5	3	0.6	66	1	0.01515	3	0	0
M3 Protostylid	2-7/0-7	10	0	0	3	0	0	6	0	0	73	7	0.09589	3	0	0
M3 Cusp 5	3-5/0-5	10	7	0.7	7	1	0.142857	7	2	0.28571	89	43	0.48315	5	0	0
M3 Cusp 6	2-5/0-5	11	0	0	8	0	0	7	0	0	96	5	0.05208	5	0	0
M3 Cusp 7	1-4/0-4	11	0	0	7	0	0	6	0	0	97	2	0.02062	5	0	0
M3 Enamel ext	1-3/0-3	11	0	0	9	0	0	4	0	0	73	5	0.06849	5	0	0
M3 Root	3/1-3	6	0	0	2	0	0	1	0	0	35	0	0	3	0	0
M3 Torsomolar angle	1/0-1	6	1	0.16667	7	0	0	2	0	0	42	0	0	2	0	0
M3 Congenital absence	1/0-1	11	0	0	9	0	0	7	0	0	57	0	0	5	0	0

Table 3. Distance values between Iberian and French (above diagonal) and the standard deviation for each distance calculation (below diagonal). The statistically significant distances are shown in bold.

	Neo MLanguedoc	Neo MProvence	Roaix	Grôtte Mykolas	Neo Solsones	Cascajos	BobM	CanSadurni	CPF
Neo MLanguedoc	-	0.047242644	**0.094119863**	0.008044099	0.041356608	**0.178357**	**0.117581514**	**0.102743424**	**0.137232021**
Neo MProvence	0.057491556	-	-0.051319028	-0.098099531	-0.060616711	-0.105925333	-0.076240671	-0.032299322	-0.016155062
Roaix	0.024332131	0.041630647	-	-0.098099531	**0.072280218**	0.039851125	0.036160317	**0.111552561**	**0.069198311**
Grôtte Mykolas	0.052906846	0.071168496	0.071168496	-	0.003814831	-0.008167946	-0.006738525	0.050240508	0.018367833
Neo Solsones	0.03573795	0.053354678	0.019470737	0.048825063	-	0.006558375	0.044313163	0.002872251	**0.110332722**
Cascajos	0.043162423	0.061176448	0.027079185	0.056597209	0.038872079	-	0.038782294	-0.011285835	-0.012858115
BobM	0.033027072	0.050611349	0.016628954	0.046049152	0.028484836	0.036127444	-	**0.063747576**	-0.0332114
CanSadurni	0.031913954	0.0493409	0.015675391	0.044755999	0.027369818	0.034766558	0.024509012	-	**0.10235459**
CPF	0.043926653	0.061408712	0.027929553	0.056834071	0.039670236	0.046936565	0.036812461	0.036021588	-

Table 4. Correlations between traits and the first to Principal Components for the analysis regarding the Iberian and French samples. The first component represents 46.95% of the variability and the second 34.65%.

	PC1 (46.95%)	PC2 (34.65%)
UM1 Hypocone	0,6571	0,7065
UM2 Metacone	-0,3564	-0,3317
UM2 Hypocone	0,6133	-0,01388
UM2 Cusp5	0,1408	-0,1247
UM2 C2 parastyle	0,3461	-0,1329
LP2 lingual cusps	0,9151	0,3651
LM1 Cusp5	-0,4178	0,9043
LM1 Cusp6	-0,5947	-0,5129
LM1 Cusp7	-0,4683	0,1919
LM2 Cusp7	-0,8296	-0,03091

Table 5. Distance values between Iberian, French, and Italian samples (above diagonal) and the standard deviation for each distance calculation (below diagonal). The statistically significant distances are shown in bold.

	UPMit	NEOit	Neo Languedoc	Roaix	Neo Solsones	Cascajos	BobM	Can Sadurni
UPMit	-	**0.191913632**	**0.478119635**	**0.42956819**	**0.599340564**	**0.573042493**	**0.372438054**	**0.411466919**
NEOit	0.023617908	-	**0.274007631**	**0.133440113**	**0.189369888**	**0.146729142**	**0.089961553**	**0.199466304**
Neo Languedoc	0.036071993	0.025371979	-	**0.166609982**	**0.087399131**	**0.232488704**	**0.251694871**	**0.31463022**
Roaix	0.022790562	0.012253844	0.024430999	-	**0.151160823**	0.039450336	**0.141709449**	0.266367032
Neo Solsones	0.040070648	0.02961417	0.04160082	0.028885383	-	0.016091129	**0.087866473**	0.067272834
Cascajos	0.050522439	0.040041146	0.052026129	0.039552085	0.056595956	-	0.000377997	0.065653546
BobM	0.033178903	0.022491478	0.034963658	0.021699342	0.039071692	0.049542787	-	**0.075247234**
Can Sadurni	0.029065851	0.018795431	0.031026192	0.018237888	0.034794576	0.04544098	0.028088038	-

Table 6. Correlations between traits and the first to Principal Components for the analysis regarding the Iberian, French, and Italian samples. The first component represents 47.1% of the variability and the second 26.9%.

	PC1 (47.1%)	PC2 (26.9%)
UI2 Shovel	-0,6408	-0,5208
UM1 Carabelli	0,7953	0,373
UM1C2 parastyle	-0,27	0,1149
UM2 Cusp5	0,9754	0,01241
LI2 Shovel	-0,3794	0,5751
LP4 lingual cusps	-0,3025	0,7732
LM1 Cusp5	0,6666	-0,537
LM1 Cusp7	-0,07293	-0,3353

Table 7. Chi square values and significance of Fisher's exact test (between brackets) for the comparison of the Montbolò sample in those traits that showed any significant difference.

	UM2 cusp5	UM2 Hypocone	LM1 cuspN	LM1 cusp5
Languedoc/Midi Pyrinées	4.937 (0.047)	.	.	.
Solsonia	8.229 (0.014)	.	.	.
Bòbila Madurell	.	8.568 (0.010)	.	.
Los Cascajos	7.467 (0.017)	4.802 (0.049)	7.368 (0.010)	20.160 (0.000)

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Heirs of the glacial maximum: Dental Morphology suggests Mesolithic human groups along the Iberian Peninsula shared the same biological origins

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Abstract

Objectives: The aim of this study is to characterise the biological diversity of the different Mesolithic communities from the various areas of the Iberian Peninsula (mainly Portuguese Atlantic Coast and Mediterranean Coast), and to provide a first glimpse in their relationships with posterior farmer groups.

Materials and Methods: The study includes 4,129 teeth belonging to a minimum of 565 prehistoric Iberian individuals of Mesolithic and Neolithic chronology (e.g. El Collado, Moita do Sebastiao, Cabeço da Arruda, La Braña, Bòbila Madurell). We analyzed the non-metric traits of these teeth with the ASUDAS methodology. Based on these phenotypic traits we estimated biological distances and compared our samples with Italian prehistoric series.

Results: Results indicated that the Mesolithic samples from the different areas Iberian Peninsula do not show significant differences between them. Moreover, the frequencies they present for most traits match the Eurodont dental complex's one. In this sense, these samples revealed to be significantly different from the Italian Palaeolithic and Mesolithic series. Finally, when compared with some Neolithic samples from the Peninsula only Mediterranean coastal samples slightly differed from the Portuguese Mesolithic groups.

Conclusions: These evidences suggest that the shared biological origin of the hunter-gatherer human groups in the Iberian Peninsula originated during the Last Glacial Maximum, as human groups took refuge in different areas of southern Europe. Furthermore, although the scenario does not seem homogeneous, the later farmer groups present an important biological influence derived from these previous samples.

Introduction

The new techniques and methodologies currently available have given a new boost to the studies carried out on materials from Mesolithic archaeological sites in the Iberian Peninsula. Many of these studies focus on the human remains found in the burial contexts from this period, which are mainly located in three areas of the Peninsula (Mediterranean coast, Cantabrian Atlantic coast, and Portuguese Atlantic coast), both isolated or forming small necropolis.

The oldest Mesolithic funerary manifestations in the Iberian Peninsula are found in the east Mediterranean area. El Collado (Valencia) is the best-known site, and provided the oldest C-14 dates for funerary contexts, 9,475-9,300 cal BC (Gibaja *et al.*, 2015). It is an open-air site where 14 sepulchres containing 15 individuals were found. Although it has the oldest dating, the funerary register of this necropolis lasted for nearly one millennium. In the same area we find the Mas Nou rock-shelter (Castellon), and the open-air site from Casa Corona (Alicante), or the Santa María cave (Aura 2010, Olaria

2010, Fernández-López et al. 2013) with a lower number of buried individuals. In the sites of Mas Nou and Casa Corona, the local hunter-gatherers would inhabit and bury some of the community's members between 8,000-7,580 cal BC (Gibaja *et al.*, 2015).

In the north of the Peninsula, most of the Mesolithic sites appear near to the Cantabrian coast of the Atlantic. The funerary contexts are shell-middens and caves that date between 7,980-6,630 cal BC, and the best-known are the Los Canes, Los Azules and La Braña caves, Aizpea rock-shelter, and the shell-midden J3 (Arias, 2007; 2013; Arias & Garralda, 1996; Barandiaran & Cava, 2001; Fernández-Tresquerres, 1997; Iriarte *et al.*, 2010; Vidal & Prada, 2010). With the exception of the 6 individuals found in Los Canes, one or two individuals were buried in each site.

Finally, several shell-middens containing tens of burials have been known in the Portuguese Atlantic coast since the 19th century. These sites are mainly found in the Sado (Sado river) and Muge (Tagus river) estuaries, and represent the largest human bone assemblages from the Mesolithic in the Peninsula. In the Muge area (estuary of River Tagus), for example, shell-middens like those of Moita de Sebastião, Cabeço da Arruda, and Cabeço da Amoreiras have surface areas of up to $3000m^2$ and a stratigraphic sequence nearly 5m thick. In Sado there are the sites of Arapouco and Cabeço das Amoreiras (Arnaud 1987, Jackes and Meiklejohn 2004, Bicho 2009, Meiklejohn et al. 2009). The oldest dates of these assemblages are those obtained for Cabeço da Arruda that situates the first inhumates in 6600-6220 cal BC. On the other hand, the C14 dates obtained for the sites from Sado (Amoreiras) estuary indicate that they were used between 6210 and 6020 cal BC (Arias, 2013; Meiklejohn *et al.*, 2009).

In most cases the individuals are buried in small pits and in a heterogeneous manner, with individuals in straight position, laid over one side of the body, and in cases like El Collado, the individuals appear hypercontracted because they were buried tied up or inside a bag (Gibaja *et al.*, 2015). None, or few grave-goods are found, with the exception of La Braña. Nevertheless, this assumption should be considered with caution, because of the contexts where the individuals were buried, caves and shell-middens, are in many cases difficult to interpret, and it is complicated to determine whether the materials surrounding the individuals were a part of the funerary ornament, or artifacts from the sedimentary deposit of the site itself. Moreover, if the grave-goods consisted of organic materials or food they would not have survived until the current time.

The first Neolithic evidence is documented from the second half of the 6th millennium BC in different parts of the Iberian Peninsula. Those communities mastered the domestication of several vegetable species (wheat, barley, peas, and beans) and animals (goats, sheep, pigs and oxen), and showed a great diversity of tools, recipients, and ornaments that were not known before. This shows that they had the knowledge to produce pottery, and the technical skills to elaborate polished axes, sculpt specific lithic and bone tools. The first burials at the first moments of the Neolithic are similar to those found in the Mesolithic period, but became actual necropolises in time.

In this context, several archaeological debates arise around a number of topics. One of them involves the biological background of the Mesolithic groups from the Iberian Peninsula, and whether they share the same origin or not. The others involve the fate of these groups, such as concerns on their role on the development of the agriculture in the Iberian Peninsula. For the former topic, there is a more homogeneous opinion, as it is believed that the Mesolithic populations are descendants of the Upper Paleolithic groups that took refuge in the Peninsula during the Last Glacial Maximum (Bañuls-Cardona *et al.*, 2014; Soomer & Nadachowski, 2006). The ancient DNA (aDNA) studies show that the Iberian Hunter-Gatherers had high frequencies of mitochondrial haplogroups H (43.8%) and U5b (37.5%), and differ from other European coetaneous groups (Szécsény-Nagy *et al.*, 2017).

On the other hand, the second issue is more controversial, and traditionally there have been two opposite stances. There were those researchers that considered that the role of the Mesolithic groups was important, as they developed the techniques due to acculturation (Tavares & Soares, 1981; Ramos *et al.*, 2006). Opposed to this were researchers like Bernabeu (2006) and Zilhao (2011) who defended a demic diffusion with an influx of already agricultural groups. The latest aDNA (Fernández-Dominguez & Reynolds 2017; Hervella *et al.*, 2012; de la Rúa *et al.*, 2015; Sampietro *et al.*, 2007; Simoni *et al.*, 2000; Szécsény-Nagy *et al.*, 2017), archaeo-botanical and faunistic (Zeder, 2008), chronometric (Isern *et al.*, 2014), and demographic (Boquet-Appel *et al.*, 2009) studies have shown that it was not a homogeneous model.

[Figure 1 here]

Like in most other prehistoric sites, teeth are the best-preserved skeletal tissues in the majority of the Mesolithic burials in the Iberian Peninsula, due to the hardness of the enamel, which is mainly of inorganic origin (95-96%) (Nanci, 2008; Simmer & Fincham, 1995). This makes them the ideal target for the study of the phenotypic relationships between the groups present in the Iberian Peninsula. Taking into account that the non-metric morphological variables of the crown and root are considered to have a high genetic control (Scott & Turner, 1997), and that teeth do not overcome modifications after they are formed, further than attrition, studying these traits might be one of the best approaches in order to characterize the biological variability in the sample. In fact, in the last decades, since the development of a standardized scoring procedure, many studies have focused on these traits in order to establish prehistoric migrations and population origins in different periods and scenarios (Coppa et al., 2007; Cucina et al., 1999; Desideri, 2007; Garcia-Sivoli, 2009; Irish, 2006; Irish et al., 2017; López-Onaindia et al., 2017; López-Onaindia et al., in press; Subirà et al., 2014).

In this work we attempt to understand the biological diversity of the Mesolithic communities from the various areas of the Iberian Peninsula, and their position in the west-European prehistory by studying their dental morphology. Moreover, we also provide a superficial survey on the relationship of these hunter-gatherer populations with the later agricultural groups.

Materials and methods

Materials

We include the analysis of 4,129 teeth belonging to a minimum of 565 prehistoric Iberian individuals (437 new and 128 already published) (Fig. 1). The samples that are novel for this work (Table 1) include Mesolithic samples from the Portuguese estuaries of Muge and Sado, Mesolithic samples from different Spanish territories (mainly Mediterranean), and the Portuguese Neolithic sample of Cabeço da Arruda (Muge).

The already published datasets from the Iberian Peninsula correspond to different Neolithic (Los Cascajos and Bòbila Madurell) and Chalcolithic (Cova del Pantà de Foix) samples (López-Onaindia & Subirà, 2017; Subirà *et al.*, 2014). Moreover, Upper Palaeolithic and Mesolithic and Neolithic samples from Italy (Coppa *et al.*, 2007) were also included in the comparison.

[Table 1 here]

Methodology

Up to 100 non-metric crown traits were scored in each dentition, according to the Arizona State University's Dental Anthropology System (ASUDAS) (Turner *et al.*, 1991). When a trait was scored in both sides of the dentition, the antimere showing the highest level of expression was counted for further analysis (Scott & Turner, 1997). It is sustained that the teeth expressing the most marked traits are the ones representing the trait's maximum potential for each individual (Turner, 1986; Turner et al., 1991). The ranked ASUDAS values for the traits were dichotomized into presence or absence values, based on their reported morphological thresholds (Nichols, 1989; Scott, 1973) according to standard procedure (Irish, 1993; Turner, 1985; 1987). From this dichotomized data, trait expression frequencies are calculated and further analyzed.

Due to the different conservation state and sample size of the collections in this study it was necessary to make diverse statistical approaches in order to analyze the relationships between the samples. The trait frequencies were analyzed using Chi-squared, with the IBM SPSS 20.00 statistics package, to study the differences between groups, trait by trait, between the Portuguese Mesolithic and Neolithic samples. Furthermore, the Mean Measure of Divergence (MMD) (Schmitt, 1972) was calculated between samples as a measure of phenetic dissimilarity. The formula used to calculate the MMD contains Freeman and Tukey's angular transformation to correct for low or high trait frequencies and small sample sizes (Harris & Sjovold, 2004). In order to determine if two samples are significantly different, the MMD has to be compared to its standard deviation (SD). Therefore, if MMD>2xSD, the null hypothesis of P1=P2 is rejected at the 0.025 level. When the internal variability of a sample is greater than that between the two samples compared, negative MMD values might result. These values are statistical artifacts, and therefore, they were set to 0 (Vargiu *et al.*, 2009; Irish, 2010). In order to avoid erroneous results in the calculation of the distances, trait edition was carried out eliminating those traits that were non-informative, and not using correlated traits (which might provoke differential weighting of the underlying dimensions on trait determination). The correlation between traits was calculated using Kendall's Tau-b analysis, and a correlation was considered strong when the Tau-b value was greater than 0.5, and for it to be statistically significant we considered that the N must be >10 and the *P* value <.05 (Irish, 2010).

Moreover, multi-dimensional scaling (MDS) (Kruskal & Wish, 1978) was used to represent the MMD distance matrixes with PAST software (Hammer *et al.*, 2001). This representation provides further information about the different relationships between sample on whether they differ significantly or not. MMD representations offer a stress value that indicates the accuracy of the same. Stress values <0.10 are usually considered excellent and ≥0.15 unacceptable (Borgatti, 1997). Finally, Principal Component Analyses (PCA) were carried out with PAST, in parallel to the MMD calculations. This analysis provides information on the traits that are more involved in the distribution observed in the MDS representation.

In some cases, the same analysis was carried out using different combinations of collections and variables in order to get a broader understanding of the interactions. Therefore, the analyses carried out were the following: 1) Chi-squared analysis between the samples from the two Portuguese Mesolithic necropolis areas (Sado and Muge estuary); 2) MMD calculation, MDS representation, and PCA analysis of Iberian (Portugal and Spain) Mesolithic, Spanish Neolithic (Bòbila Madurell, Cascajos) and Chalcolithic (Cova del Pantà de Foix), and Italian Mesolithic and Neolithic samples based on 4 non-metric traits; 3) calculation of MMD distance matrix excluding the Italian samples, in order to contrast the previous results based on 11 non-metric traits; 4) this time the excluded sample was the Spanish Mesolithic, and the MMD calculation was based on 22 variables; this matrix was represented in an MDS, and the PCA analysis was also carried out; 5) finally, the relationship between the Portuguese Neolithic sample (Algar do Bom Santo) and the Mesolithic ones was tested by MMD calculation and its MDS representation, as well as PCA analysis. For this latter MMD and PCA analysis, Neolithic and Chalcolithic samples from Spain were also used, and they were based on 8 non-metric traits.

[Table 2 here]

Results

The amount of teeth scored for each trait and the frequencies of these in the different samples analyzed for the study are shown in Table 2 (2.1 and 2.2). The dichotomic cut-off point for each of the trait is also provided in the Table. Moreover, it can be observed that many traits have been observed less than 10 times in some samples, which limits using them in further analyses.

As the Mesolithic sample from Sado estuary is small and there are not many traits observed more than 10 times, Fisher's exact test analysis was used to test whether it showed differences with the Muge estuary's Mesolithic sample and if both could be combined for further analysis. The results of this test show that there are no significant differences in any of the traits compared between the two samples, and therefore can be combined to compare them with other samples.

[Table 3 here]

The results obtained from Kendall's Tau-b analysis to identify correlated traits showed that several traits were significantly correlated. Specifically, *UM2 Cusp5* was correlated to the following traits: *UP4m&d cusps* (Tau-b= 0.687; N= 19), *UM3 Cusp5* (Tau-b= 0.642; N= 19); *LM1 Cusp5* (Tau-b= 0.565; N= 16); and *LM3 Protostylid* (Tau-b= 0.746; N= 13). Furthermore, *UM3 C2 Parastyle* was found to be correlated with: *UM3 Cusp5* (Tau-b= 0.689; N= 17), and *UP4 m&d cusps* (Tau-b= 0.602; N= 13). *LC DAR* was found to be correlated with two other traits: *UM3 Carabelli* (Tau-b= 0.725; N= 11), and *UM1 Metacone* (Tau-b= -0.566; N= 18). Finally *LM1 Cusp5* and *UM2 Metacone* also appear to be inversely correlated (Tau-b= -0.542; N= 16).

The MMD analysis based on 4 traits, with the two Iberian Mesolithic samples, two Iberian Neolithic (Bòbila Madurell and Los Cascajos), and the Chalcolithic (Cova del Pantà de Foix). Samples from Spain and Italian Mesolithic and Neolithic samples (Table 3) show that there are no significant differences between the Iberian samples, but that all of them are significantly different from the Italian ones. Nevertheless, it also shows that there are no significant differences between the Italian Mesolithic and Neolithic, which contradicts previous works using more variables in the analysis.

The MDS representation of the distance matrix (Fig. 2) shows two main separate groups: Italians and Iberians. Among the Iberian samples, Bòbila Madurell (Neolithic Mediterranean) is the most distant from the rest of the samples, together with the Portuguese Mesolithic one. The PCA analysis shows a similar sample dispersion pattern (not shown) to the one obtained in the MDS, and the first two components explain about 97% of the total observed variation. The Italian samples are characterized by higher frequencies of *LM2 Cusp6* and *LM3 Protostylid*, compared to all the Iberian ones. Furthermore, the differences between the Iberian Mesolithic and Neolithic samples rely on greater frequencies of *LM2 Cusp Number* for the former, while the latter has higher frequencies of *UP3 Cusps*.

[Figure 2 here]
[Table 4 here]

The previous results were based on a small amount of variables, which in the case of the Italian samples, contradicts previous works. Taking this into account, further analysis were carried out without the Italian series in order to check if the phenotypical interactions between the samples from the Iberian Peninsula were reliable and replicable when analyzing more traits. Therefore, the MMD distances calculated between the Iberian samples (Table 4) are based on 11 traits, and show that there are no significant differences between the two Mesolithic samples, and that the only comparisons showing significant differences are those that involve the Portuguese Mesolithic sample compared to Bobila Madurell and Cova del Pantà de Foix, the two samples from the Mediterranean coast. The MDS representation of these results is not provided because it is associated with a stress value of 0.37.

[Table 5 here]

We performed another comparison to determine whether these differences were consistent, as well as to observe the affinities of the Neolithic groups from the Iberian Peninsula. This analysis included the Italian samples and excluded the Spanish Mesolithic one -which was the one limiting the number of traits that could be used for the analysis – and was based on 22 traits. The results (Table 5) show that both Italian samples diverge significantly from all the Iberian groups and between them, while the sole comparison among Iberian groups that shows significant differences is between the Italian Mesolithic and Bòbila Madurell samples.

[Figure 3 here]

The MDS representation (Fig. 3) illustrates a similar scenario to that seen in the previous one, where two groups seem to appear: the Iberian and the Italian. In this case, it can be observed that both Mesolithic groups are the most separated among all samples, and that the Neolithic samples from both peninsulas appear more centred in the plot. The PCA analysis provides a similar representation to the MDS, where the two first components represent 80% of the total variation. Moreover, the traits correlation with each Principal Component (Table 6) show that the Italian samples presented significantly higher frequencies of *UM3 Carabelli's Cusp*, *UM3 Cusp5*, *UM1 Carabelli's Cusp*; *UM3 Hypocone*, *LM2 Cusp6*, *UI2 Interruption Groove*, and *LM1 Cusp5*; while the Iberian traits where characterized by greater frequencies of *LP4 lingual cusps* and *Shovelling of UI2 and LI2*.

The last set of analyses, based on 9 traits and aimed at checking whether the Neolithic sample of Algar do Bom Santo (Portugal) is related to the Mesolithic sample from Portugal and the rest of Iberian samples, shows that the only significant distance value is the one involving the Portuguese Mesolithic and Bòbila Madurell samples (Table 7). Although the stress level for the MDS representation (Fig. 4) is high (0.1907), it shows some tendencies similar to previous analysis, where the samples from the Mediterranean (Bòbila Madurell and Cova del Pantà de Foix) appear more distant from the rest. Nevertheless, it is not exactly the same, because the Mesolithic sample is situated on its own in one corner of the plot, with the Mediterranean samples (Bòbila Madurell and Cova del Pantà de Foix) in the opposite extreme of the plot. Meanwhile, Los Cascajos and the Portuguese Neolithic samples stand in the middle of them. In the PCA analysis (plot not included) the first two components represent 84% of the total variability. The traits responsible for the main differentiation between the Mesolithic sample and the two Mediterranean samples are the higher presence of *UM2 Cusp5* and *LM1 Cusp N* (more than 5 cusps) in the latter group, while the Mesolithic sample had a higher frequency *UM2 Metacone* (Table 8).

[Table 6 here]
[Table 7 here]
[Figure 4 here]
[Table 8 here]

Discussion

Our results suggest that the Mesolithic samples from the different areas of the Iberian Peninsula were biologically alike between them, as no significant differences have been found in the several analysis carried out involving these samples (Fisher's exact test, MMD calculation, and PCA analysis). This homogeneity of the pre-Neolithic Iberian samples might be a consequence of the events that occurred during the Last-Glacial maximum, when the Iberian Peninsula, Italian Peninsula and Southeast Europe became habitable refuges in the otherwise harsh continent (Sommer & Nadachowski, 2006). As result, the population of the Iberian Peninsula would be isolated, and once the climate softened that group would have expanded and spread both in the peninsula itself and colonized different European areas (Achili *et al.*, 2004; Torroni *et al.*, 1998; 2001; Wiik, 2008).

Moreover, the Iberian Mesolithic sample is also significantly different from the Italian Hunter-Gatherer sample. Although the analysis where both Portuguese and Spanish samples are included based on a small number of variables and that the relationship between Italian pre-Neolithic and Neolithic samples differed from Coppa and collaborators (2007), the results obtained are compatible with those suggested by the remaining analyses carried out, where either the Italian samples or the Spanish Mesolithic were removed in order to increase the number of analyzed traits. In the analysis based on 22 traits (the results are shown in Table 5) the most different samples between them are the Portuguese and Italian Hunter-Gatherers. This result is consistent with the latest ancient DNA studies in the Iberian Peninsula, which suggest that the Iberian group differs from other European pre-Neolithic samples (de la Rua *et al.*, 2015; Szécsény-Nagy *et al.*, 2017). This difference is based on the high frequency of mitochondrial haplogroup H detected in the Iberian sample, and the extremely low frequencies of haplogroups U2 and U5a, which are usual in other continental haplogroups.

In addition, some of the traits that correlate most with this differentiation between the groups of the two peninsulas, and more remarkably the pre-Neolithic samples, have been highlighted in relation to the description of the Eurodont Dental Complex in modern populations from the Iberian Peninsula (Scott *et al.*, 2013). The high rate of multi-cusped LP4 (*LP4 lingual cusps*) is a trait considered in this complex, as it is the low frequency of five cusped lower molars. Furthermore, the Portuguese Mesolithic sample shows frequencies similar to those described for the complex in most traits, and in some cases they are more extreme (as the case of lower *UM1 Cusp 5*, *UI2 Tuberculum dentale* and *LM1 Cusp 6* frequencies). The only trait where it does not match the expected ratio is *UM1 Carabelli's Cusp*, which is high in Eurodont samples and low in Iberian Mesolithic samples.

The Neolithisation process is believed to have been complex in the Iberian Peninsula according to genetic, faunistic, and botanic data (de la Rúa *et al.*, 2015; Szécsény-Nagy *et al.*, 2017; Zeder, 2008). The oldest evidences of domesticated plants and animals are found in the Mediterranean area in the 6th millennium BC, and therefore is believed that it started following interactions along the western Mediterranean coast of Europe (Oms *et al.*, 2016), while the evidence of productive practices in the Northern and Southwestern Atlantic coast are a bit younger (Fernández-Eraso *et al.*, 2015). In this sense, the genetic studies detect signals of admixture or prevalence of Mesolithic individuals in the Early and Middle Neolithic samples of the Iberian Peninsula, detected by the high ratios of mtDNA haplogroup H (Szécsény-Nagy *et al.*, 2017), and the low ratios of J and U haplogroups (de la Rúa *et al.*, 2015). The signal, nevertheless differs in the different areas, and while in the Mediterranean area the pre-Neolithic haplogroups are less frequent (Sampietro *et al.*, 2007, Szécsény-Nagy *et al.*, 2017), in the North of the Peninsula and in the Portuguese Atlantic area, the ratios are higher (Hervella *et al.*, 2012; Pereira *et al.*, 2017; de la Rúa *et al.*, 2015; Szécsény-Nagy *et al.*, 2017). Our results suggest continuity in the biological background of the Neolithic populations compared to the Mesolithic in the Iberian Peninsula, although with observations. The first of these observations is that it is only a shallow approach to this discussion, and more samples should be analyzed in the future. The only Neolithic sample that shows significant differences with the Mesolithic samples from the Iberian Peninsula is Bòbila

Madurell. At the same time, this Neolithic sample does not show significant differences with any of the other Neolithic and Chalcolithic samples from the Peninsula, although it is significantly different from the Italian groups. Nevertheless, despite being significantly different from the Italian samples, it is the one that diverges less from them. We interpret these results as indicators of differential influence of incoming populations in the development of the Neolithic in different areas of the Peninsula. Although Los Cascajos does not significantly diverge from the Mesolithic Iberian samples, its distance value with the Italian Neolithic is also smaller. This might be indicative of some small biological influence of incoming farmer groups in this area, and smaller to that found in areas closer to the Mediterranean.

Taking into account that our results coincide in the major lines with those obtained with DNA analyses, shows that the application of dental morphology studies to population relationships is valid. Hubbard *et al.* (2015) already reported that biological distance matrixes obtained by studying dental morphology correspond to those obtained analyzing nuclear DNA in modern Kenyan populations. In this work, they show that both methods identify greater divergence among samples from different ethnic groups, although the genetic data provides finer resolution in the among-population relationships, which also seems to be happening in the current case.

To summarize, our data concurs with the data obtained by DNA analysis in the same study area. Therefore, the present study identifies that the Mesolithic populations from the Iberian Peninsula had a homogeneous biological background, which diverged from the biological background of the Italian Hunter-Gatherers, probably due to separation during the Last Glacial Maximum. Moreover, the recorded trait frequencies are almost compatible with the Eurodont Dental Complex. Finally, we observed that, although the scenario is not homogeneous, there is a large biological influence of the Mesolithic groups in the subsequent Neolithic ones.

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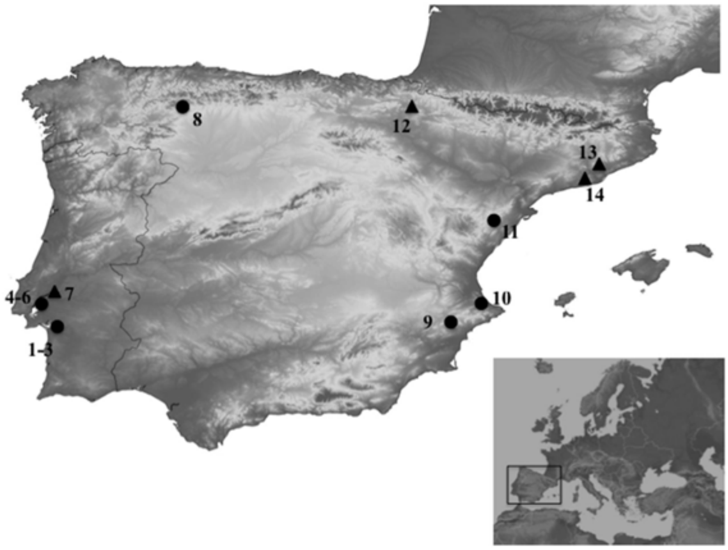
Figure 1. Location of the sites included in the study. 1-3: Sado Mesolithic (Arapouco, Cabeço das Amoreiras, Cabeço do Pez; 4-6: Muge Mesolithic (Moita do Sebastiao, Cabeço da Arruda, Cabeçp da Amoreira); 7: Algar do Bom Santo; 8: La Braña-Arintero; 9: Casa Corona; 10: El Collado, 11: Masnou; 12: Los Cascajos; 13: Bòbila Madurell; 14: Cova del Pantà de Foix. Mesolithic samples are represented by dots, and Neolithic samples by triangles.

Figure 2. MDS representation of the MMD matrix based on 4 traits. The stress value for this representation is 0.2056. MESport: Mesolithic Portugal; MESesp: Mesolithic Spain; Cas: Los Cascajos; BobM: Bòbila Madurell; CPF: Cova del Pantà de Foix; UPMit: Italian Upper Palaeolithic and Mesolithic; NEOit: Italian Neolithic.

Figure 3. MDS representation of the distance matrix involving Iberian Peninsula's samples and Italian samples based on 22 traits. The stress value associated to this representation is 0.0635. MESport: Mesolithic Portugal; Cas: Los Cascajos; BobM: Bòbila Madurell; CPF: Cova del Pantà de Foix; UPMit: Italian Upper Palaeolithic and Mesolithic; NEOit: Italian Neolithic.

Figure 4. MDS representation of the MMD matrix involving Iberian samples and based on 9 traits. The stress value for this representation is 0.1907. MESport: Mesolithic Portugal; NEOport: Neolithic Portugal; Cas: Los Cascajos; BobM: Bòbila Madurell; CPF: Cova del Pantà de Foix.



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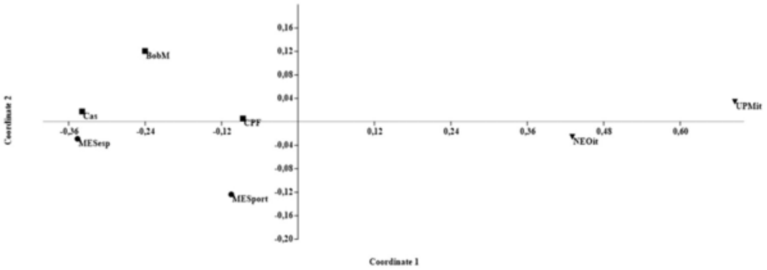

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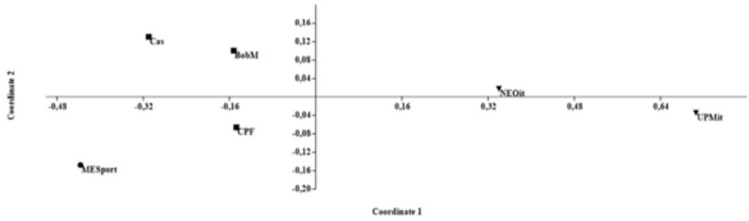

Figure 3. MDS representation of the distance matrix involving Iberian Peninsula's samples and Italian samples based on 22 traits. The stress value associated to this representation is 0.0635. MESport: Mesolithic Portugal; Cas: Los Cascajos; BobM: Bòbila Madurell; CPF: Cova del Pantà de Foix; UPMit: Italian Upper Palaeolithic and Mesolithic; NEOit: Italian Neolithic.

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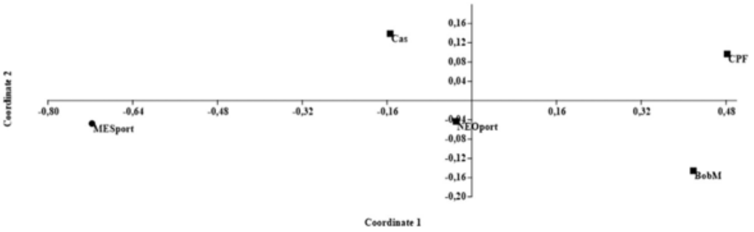

Figure ¬4. MDS representation of the MMD matrix involving Iberian samples and based on 9 traits. The stress value for this representation is 0.1907. MESport: Mesolithic Portugal; NEOport: Neolithic Portugal; Cas: Los Cascajos; BobM: Bòbila Madurell; CPF: Cova del Pantà de Foix.

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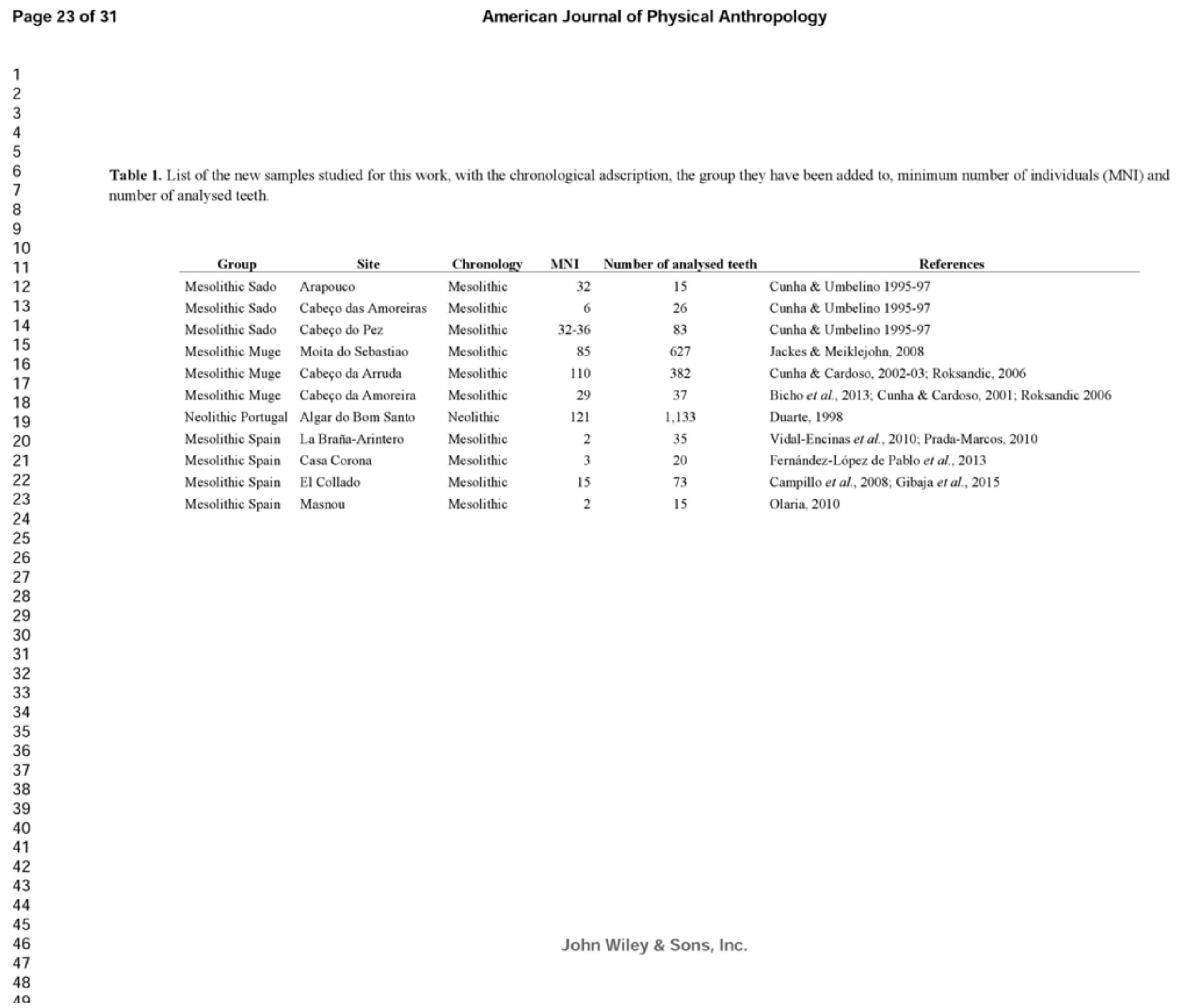

Table 1. List of the new samples studied for this work, with the chronological adscription, the group they have been added to, minimum number of individuals (MNI) and number of analysed teeth.

Group	Site	Chronology	MNI	Number of analysed teeth	References
Mesolithic Sado	Arapouco	Mesolithic	32	15	Cunha & Umbelino 1995-97
Mesolithic Sado	Cabeço das Amoreiras	Mesolithic	6	26	Cunha & Umbelino 1995-97
Mesolithic Sado	Cabeço do Pez	Mesolithic	32-36	83	Cunha & Umbelino 1995-97
Mesolithic Muge	Moita do Sebastiao	Mesolithic	85	627	Jackes & Meiklejohn, 2008
Mesolithic Muge	Cabeço da Arruda	Mesolithic	110	382	Cunha & Cardoso, 2002-03; Roksandic, 2006
Mesolithic Muge	Cabeço da Amoreira	Mesolithic	29	37	Bicho *et al.*, 2013; Cunha & Cardoso, 2001; Roksandic 2006
Neolithic Portugal	Algar do Bom Santo	Neolithic	121	1,133	Duarte, 1998
Mesolithic Spain	La Braña-Arintero	Mesolithic	2	35	Vidal-Encinas *et al.*, 2010; Prada-Marcos, 2010
Mesolithic Spain	Casa Corona	Mesolithic	3	20	Fernández-López de Pablo *et al.*, 2013
Mesolithic Spain	El Collado	Mesolithic	15	73	Campillo *et al.*, 2008; Gibaja *et al.*, 2015
Mesolithic Spain	Masnou	Mesolithic	2	15	Olaria, 2010

Table 2.1. Sample sizes (N), presence recount (Presence), and dichotomic breaking points for the studied maxillary traits.

		Mesolithic Sado		Mesolithic Muge		Neolithic Muge		Mesolithic Spain	
Trait	**Breaking point**	N	Presence	N	Presence	N	Presence	N	Presence
I1 Labial curve	1/1-4			16	0				
I1 Interrup. Groove	1/0-1			21	1			6	1
I1 Shovel	3-6/0-6			12	2			6	1
I1 Double shovel	2-6/0-6			21	2			6	1
I2 Interrup. Groove	1/0-1			28	6	2	0	9	1
I2 Shovel	3-7/0-7			17	5	2	1	7	2
I2 Double shovel	2-6/0-6			24	5	4	0	9	1
I2 I & C t.d.	2-6/0-6			11	1	1	0	7	1
I2 Peg (<7)/reduce	2/0-2							2	0
I2 cong absence	1/0-1			49	0	5	0	4	0
C I & C t.d.	2-6/0-6			19	14	2	1	8	1
C mesial ridge	2-5/0-5			18	3	1	0	8	1
C Dist. access ridge	2-5/0-5			15	2	1	1	6	2
P3 m&d cusps	1/0-1			29	1	3	1	10	1
P4 m&d cusps	1/0-1			29	1	6	3	7	0
M1 Metacone	2-5/0-5	4	4	64	64	5	5	8	8
M1 Hypocone	2-5/0-5	3	3	61	61	3	3	10	10
M1 Cusp 5	1-5/0-5	4	0	48	1	8	0	10	3
M1 Carabelli	2-7/0-7	4	0	22	7	7	1	9	1
M1 C2 parastyle	1-5/0-5	4	0	43	0	7	0	9	1
M2 Metacone	2-5/0-5	5	5	56	56	11	11	8	8
M2 Hypocone	2-5/0-5	4	4	46	38	9	9	10	10
M2 Cusp 5	1-5/0-5	5	0	49	5	12	0	9	2
M2 Carabelli	2-7/0-7	5	0	32	1	11	0	9	1
M2 C2 parastyle	1-5/0-5	4	0	51	3	11	0	10	1
M3 Metacone	2-5/0-5	3	3	37	37	5	5	7	6
M3 Hypocone	2-5/0-5	3	3	38	17	3	2	9	5
M3 Cusp 5	1-5/0-5	3	0	36	8	5	0	9	4
M3 Carabelli	2-7/0-7	2	0	29	1	4	0	9	1
M3 C2 parastyle	1-5/0-5	2	0	27	2	5	0	9	1
M3 cong. Absence	1/0-1	3	0	47	0	5	0	2	0

Table 2.2. Sample sizes (N), presence recount (Presence), and dichotomic breaking points for the studied mandibular traits.

		Mesolithic Sado		**Mesolithic Muge**		**Neolithic Muge**		**Mesolithic Spain**	
Trait	**Breaking point**	N	Presence	N	Presence	N	Presence	N	Presence
I1 Shovel	2-3/0-3	3	0	28	0			2	0
I2 Shovel	2-3/0-3	5	0	31	1			7	0
C Dist. access ridge	2-5/0-5	3	1	21	4			4	0
P3 lingual cusps	2-9/0-9	1	1	31	8			7	3
P4 lingual cusps	2-9/0-9	1	0	30	19			5	0
M1Groove pattern	Y/Y,+,X	3	1	26	15	5	1	3	2
M1 Cusp nº	6-7/4-7	8	0	53	1	12	1	10	0
M1 Def Wrinkle	2-3/0-3	3	2	9	5	5	0	6	0
M1 Distal crest	1/0-1	4	0	13	0	5	0	4	0
M1 Protostylid	2-7/0-7	7	0	37	1	12	0	8	0
M1 Cusp 5	3-5/0-5	9	5	52	42	12	6	7	3
M1 Cusp 6	2-5/0-5	9	0	48	0	12	1	9	0
M1 Cusp 7	1-4/0-4	9	0	56	0	12	1	9	0
M2 Groove pattern	Y/Y,+,X	5	3	51	11	5	4	7	2
M2 Cusp nº	4/4-6	9	9	59	57	9	9	11	11
M2 Def Wrinkle	2-3/0-3	4	1	12	5	5	0	8	0
M2 Distal crest	1/0-1	4	0	33	0	6	0	8	1
M2 Protostylid	2-7/0-7	7	0	41	0	8	0	9	0
M2 Cusp 5	3-5/0-5	9	0	58	2	9	1	9	3
M2 Cusp 6	3-5/0-5	9	1	59	0	9	0	10	0
M2 Cusp 7	1-4/0-4	9	0	58	0	9	0	10	0
M3 Groove pattern	Y/Y,+,X	3	3	34	17	4	2	6	1
M3 Cusp nº	4/4-6	7	6	38	27	6	5	9	9
M3 Def Wrinkle	2-3/0-3	3	0	8	4	5	0	5	1
M3 Distal crest	1/0-1	4	0	24	0	5	0	7	3
M3 Protostylid	2-7/0-7	6	0	30	3	6	1	10	0
M3 Cusp 5	3-5/0-5	7	1	37	8	6	1	10	3
M3 Cusp 6	2-5/0-5	7	1	38	0	6	0	9	1
M3 Cusp 7	1-4/0-4	7	0	38	0	6	1	9	0
M3 Torsomolar angle	1/0-1	6	0	28	1	3	0		
M3 Cong. Absence	1/0-1	8	0	44	0	6	0		

Table 3. Matrix showing the MMD distances between the analysed samples (upper diagonal) and the standard deviation for each distance (lower diagonal), based on 4 traits. The significant distances are marked in bold.

	MESport	MESesp	BobM	Cas	CPF	UPMit	NEOit
MESport	-	0	0.094477839	0.06042736	0	**0.893776481**	**0.569961538**
MESesp	0.08222922	-	0	0	0	**1.122404958**	**0.782098643**
BobM	0.039126255	0.087862097	-	0	0	**0.945901149**	**0.660921397**
Cas	0.072464902	0.120699495	0.077775212	-	0	**1.066903347**	**0.734791515**
CPF	0.060310951	0.107639857	0.065183459	0.098530549	-	**0.767461082**	**0.472722396**
UPMit	0.039482202	0.087553201	0.044277378	0.077621476	0.065620983	-	0.026770922
NEOit	0.027343808	0.075853273	0.032506355	0.065803932	0.053545594	0.032742028	-

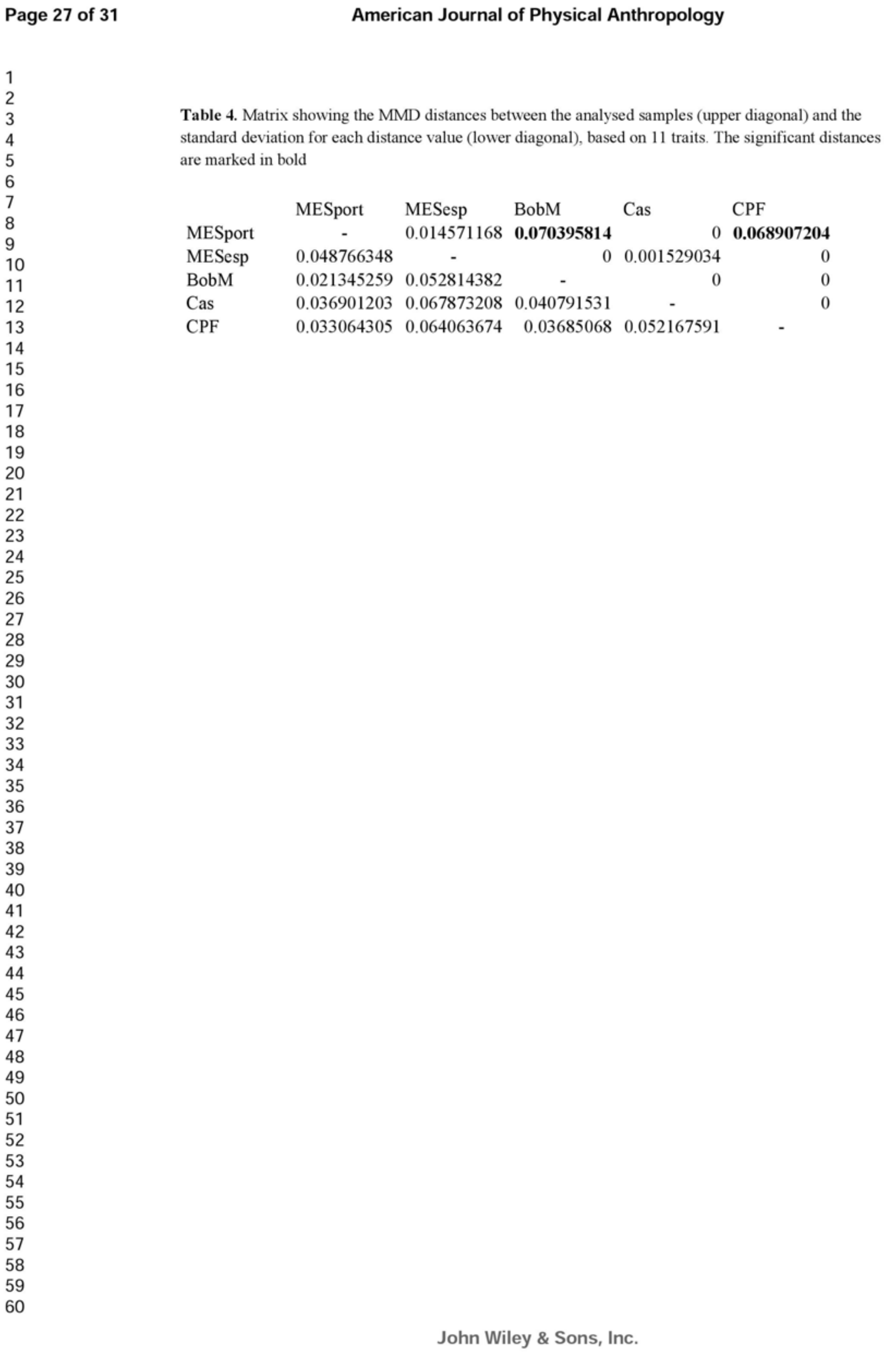

Table 4. Matrix showing the MMD distances between the analysed samples (upper diagonal) and the standard deviation for each distance value (lower diagonal), based on 11 traits. The significant distances are marked in bold

	MESport	MESesp	BobM	Cas	CPF
MESport	-	0.014571168	**0.070395814**	0	**0.068907204**
MESesp	0.048766348	-	0	0.001529034	0
BobM	0.021345259	0.052814382	-	0	0
Cas	0.036901203	0.067873208	0.040791531	-	0
CPF	0.033064305	0.064063674	0.03685068	0.052167591	-

Table 5. Matrix showing the MMD distances between the analysed samples (upper diagonal) and the standard deviation for each distance value (lower diagonal), based on 22 traits. The significant distances are marked in bold.

	MESport	BobM	Cas	CPF	UPMit	NEOit
MESport	-	**0.074282392**	0.022460984	0.006449324	**0.299579158**	**0.158076311**
BobM	0.020835743	-	0	0	**0.228274547**	**0.084582006**
Cas	0.032289524	0.035143126	-	0	**0.284673476**	**0.107278049**
CPF	0.030254102	0.032858783	0.044195041	-	**0.219995729**	**0.081719346**
UPMit	0.020109218	0.022327134	0.033742211	0.031614983	-	**0.072720205**
NEOit	0.014006469	0.016473459	0.02793755	0.025774974	0.01553209	-

Table 6. Correlation values for the traits regarding each of the first two Principal Components. Although the distribution in the PCA analysis is similar to that in the MDS, it is important to mention that the Iberian samples locate in inverse position compared to it.

	PC1 (64.8%)	PC2 (15.2%)
UI2InterGroove	0.8095	-0.5451
UI2Shovel	-0.7638	0.2782
UCDAR	0.624	-0.4592
UP3Cusps	0.1262	-0.7213
UP4Cusps	-0.1005	-0.6129
UM1Carabelli	0.9142	-0.07318
UM1C2Parastyle	-0.04436	-0.1295
UM3Hypocone	0.9025	0.1213
UM3Cusp5	0.9728	0.192
UM3Carabelli	0.9804	0.07853
LI2Shovel	-0.8193	-0.2881
LP4Cusps	-0.8756	-0.3372
LM1Groove	0.5389	-0.71
LM1Cusp5	0.7444	0.469
LM1Cusp7	0.06704	-0.5404
LM2Groove	0.1488	0.5752
LM2CuspN	-0.1994	0.7419
LM2Cusp5	0.6879	-0.3123
LM2Cusp6	0.8287	0.3026
LM3Groove	-0.6503	0.5296
LM3CuspN	-0.1663	0.7198
LM3Cusp7	0.4284	-0.1631

Table 7. Matrix showing the MMD distances between the analysed samples (upper diagonal) and the standard deviation for each distance value (lower diagonal), based on 9 traits. The significant distances are marked in bold.

	MESport	NEOport	BobM	Cas	CPF
MESport	-	0.0211641	**0.05767645**	0	0.076725046
NEOport	0.050800908	-	0	0	0
BobM	0.023911988	0.055716723	-	0.01510183	0
Cas	0.03777218	0.069214932	0.042588696	-	0
CPF	0.036328631	0.067849104	0.041005383	0.054229375	-

Table 8. Correlations between traits and the first to Principal Components for the analysis regarding the Iberian samples with the Neolithic Portuguese series.

	PC1 (62.5%)	PC2 (22.6%)
UM2Metacone	-0.9659	0.1393
UM2Cusp5	0.9422	0.3344
UM2Carabelli	0.3678	0.45
UM2C2Parastyle	0.487	0.7272
LM1CuspN	0.9016	-0.3961
LM1Protostylid	-0.4212	0.6312
LM1Cusp6	0.3222	-0.8868
LM1Cusp7	-0.4504	-0.4135

Evidences of Hunter-Gatherer biological profile retention in Farmer populations from the Iberian Peninsula based on Dental non-metric trait analysis

Diego López-Onaindia, Juan F. Gibaja, M. Eulàlia Subirà

Abstract

The origin of the Neolithic culture in the Iberian Peninsula has been a subject of debate for decades. New analyses are showing that this process was rather complex, compared to what was thought before. In this work we present the analysis of biological affinities based on dental morphology of Pre-Neolithic Hunter-Gatherers and Neolithic and posterior groups. We have analysed the teeth of at least, 1,184 individuals, on what it is the study with a larger sample size analysed by a single methodology around this subject. Our results suggest that although there were possibly two entrance areas for farmer populations in the Peninsula (from the east, through the Mediterranean; and from the North across the Pyreneans), populations descendent of the previous Mesolithic groups persisted. Moreover, the influence of these groups in the biological profile of farmer populations increased after the Middle-Neolithic.

Introduction

The first evidences of the change from Hunter-Gatherer lifestyle to productive ways of subsistence have been recorded in the Near East, and date back to around 10,000 BCE (Bellwood, 2005; Özdogan, 1997). During the 7th and 6th millennia BCE the farming techniques and related pottery spread to the West and North, through Europe. Overall, it is accepted that this process started in the Balkans to the North, to Central Europe; and along the Mediterranean coast throughout Greece, Italy and South of France, from where it would took North to the Paris basin and South to the Iberian Peninsula (Zilhão, 2001).

Taking into account the archaeological evidences, there seems to be two separate events that influenced the development of the Neolithic in the Iberian Peninsula, and Northwestern area of the Mediterranean overall (García-Martínez de Lagrán, 2015). The oldest evidences of a productive society in the Peninsula are found around 5,800 cal BCE, in Guixeres de Vilobí and El Barranquet sites (Bernabeu et al., 2011; Oms et al., 2014), East of the Peninsula. These evidences would be related to pottery with *Impressa-Ligur* style decoration.

The second event is related to the discovery of Cardial decoration in the pottery, which is documented after 5,600-5,500 cal BC (Guilaine et al., 2007; Oms et al., 2016; Rojo et al., 2015). The sites that represent this moment are also found near the coastal and pre-coastal areas of the Northwest Mediterranean, and also in inland areas in isolated cases.

During this early Neolithic period the dominant elements in the economy were ovicaprids (*Ovis* and *Capra*) (Saña, 2013), different types of naked wheat (*Triticum disccocum/ aestivun/durum*) and barley (*Hordeum vulgare*) (Bernabeu et al, 2011; Guilaine et al., 2007; Oms et al., 2014).

Nevertheless, this lifestyle substitution was not homogeneous in the Peninsula, and Hunter-Gatherer and Farming groups coexisted and interacted for as long as two millennia (Jimenez-Guijarro, 2010). This fact lies out that the process was complex, as it has been suggested by chronological, demographic, cultural, botanic, faunistic and genomic data (Boquet-Appel et al., 2009; Gamba et al., 2012; Fernández-Domingez & Reynolds, 2017; Hervella et al., 2012; Isern et al., 2014; de la Rúa et al., 2015; Sampietro et al., 2007; Simoni et al., 2000; Szécsény-Nagy et al., 2017; Zapata et al., 2014; Zeder, 2008).

In the concrete case of funerary sites, and therefore, human osteological material, during the Upper Palaeolithic most were found in the North and Northeast of the Iberian Peninsula. In contrast, during the Mesolithic there were three main areas where burials have been found: the Mediterranean area; Portuguese Atlantic coast; and the Cantabrian Fringe. The oldest Mesolithic burials in the Peninsula are found in El Collado, in the Mediterranean area (Aparicio, 2008; Aura, 2010; Fernández-López et al., 2013; Gibaja et al., 2015; Olaria, 2010). The burials from the Portuguese Atlantic coast mainly took place in small caves and rock-shelters from Muge and Sado estuaries, and hundreds of individuals have been recovered from them (Arias, 2013; Meiklejohn *et al*., 2009). Finally, the most recent evidences of Mesolithic burials are found in the Cantabrian Fringe, such as the Burials of Los Canes and La Braña (Arias, 2007, 2013; Arias and Garralda, 1996; Barandiaran and Cava, 2001; Fernández-Tresguerres, 1997; Iriarte et al., 2010; Vidal & Prada, 2010).

Funerary manifestations during the Early Neolithic in the Northeast of the Peninsula are scarce (Bosch & Tarrús 1991; Blasco et al. 2005; Gonzalez et al. 2011; Oms et al. 2017), and it was after the second half of the 5th millennium BCE that the situation started to change as a proliferation of funerary evidence became evident. This bloom in the number of structures aimed to inhumate individuals occurred specially in the Northeast of the Peninsula, either in the form of necropolises or as isolated burials (Gibaja et al. 2016 a; Gibaja & Clop, 2012; Martín 2009). While during the Early Neolithic most burials occurred in caves or in simple pits in open-air sites, during the Middle-Neolithic there were no inhumations in caves. Nevertheless, new modalities appeared in concrete areas, such as the stone-cists in the Pre-Pyrenean and Pyrenean areas of Catalonia. In most cases, during this period the graves consisted on primary burials that contained a single individual, but in some cases they could contain three or more individuals (Allièse et al., 2014).

During the Late-Neolithic and Chalcolithic (mid-late 4th millennium cal BCE) collective burials were most common. This seems to have been related to a demographical increase, to a change in settlement patterns, and to the exchange networks established between groups from the western Mediterranean. These inhumations were mainly carried out in dolmens closed by a tumulus, or by using free space in caves.

Teeth are the best-preserved skeletal remains in most of the contexts from this period in the Iberian Peninsula as taphonomic effects affect them less, mainly due to the mostly inorganic composition of enamel (Nanci, 2008; Simmer & Fincham, 1995). This makes teeth the ideal target for studying phenotypic relationships between Hunter-Gatherer and Farming groups in the Iberian Peninsula. Moreover, teeth do not overcome changes, other than attrition, after formation. As this process occurs early in life, the time spam in which environmental factors might interact with the genetic information leading formation is reduced. Therefore, it is believed that tooth development has a higher genetic influence than other elements. Concretely, the discrete traits (cusps, tubercles, grooves, etc.) of the teeth present an important heritable nature (Scott & Turner, 1997). The heritage pattern for most of the traits is still unknown, but is presumably multigenic (Scott & Turner, 1997; Hughes & Townsend, 2013). Furthermore, it has been suggested that these morphological traits of teeth do not show sexual dimorphism (Scott & Turner, 1997), and they usually respond to neutral selection (Manabe *et al*., 2011).

This methodology has been proved successful in determining population affinities, origin and migrations in different prehistoric and historic scenarios (Coppa et al., 2007; Desideri, 2011; Irish, 2006). The studies in remains from the Iberian Peninsula are scarce, although they have increased during the last years (Cerepuelo et al., 2015; Desideri, 2011; Garcia-Sivoli, 2009; Irish et al., 2017; Laguillo et al., 2009; Rivera-Garcia, 2012; Scott et al., 2013). In previous works of our group, we have studied the relationships between samples from each of the periods in order to determine the diversity during the Mesolithic and the Neolithic (López-Onaindia & Subirà, 2017; López-Onaindia et al., in press; López-Onaindia et al., submitted a; López-Onaindia et al., submitted b; Pascual et al., 2016; Subirà et al., 2016). The results obtained in these works have provided the necessary information in order to organise the samples for the current work.

The aim of this work is to analyse the complex transition to productive societies in the Northeast of the Iberian Peninsula using dental morphology in order determine biological relationships between samples. This work presents the larger number of individuals analysed with a single methodology in this subject to date. Therefore, pretends to sum in the vast amount of works being carried out involving aDNA and chronology and shed some light onto the debate.

Materials and Methods

Non-metric data of 15,145 teeth of at least 1,184 prehistoric individuals from the Iberian Peninsula and Southern France are included in this work; data of 195 of these individuals are novel in this work (Figure 1). These individuals represent Upper-Palaeolithic, Mesolithic, Early- and Middle-Neolithic, Late-Neolithic/Chalcolithic, and Bronze Age inhabitants of these regions.

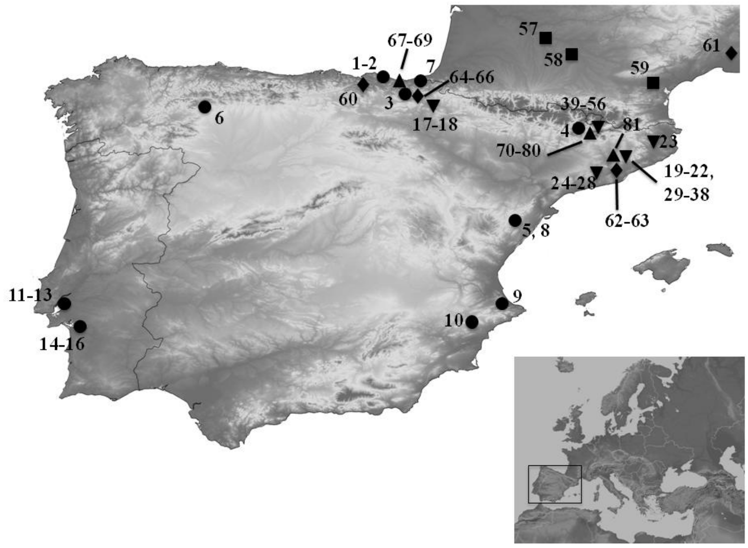

Figure 1. Location of the 81 sites analysed for this study. Dots indicate Palaeolithic and Mesolithic sites; inverted triangles are used for Early- and Middle-Neolithic sites from the Iberian Peninsula; squares represent Middle-Neolithic samples from Midi-Pyrennées/Languedoc area; diamonds indicate Late-Neolithic and Chalcolithic sites; and triangles were the Bronze Age sites. The numbers for each site correspond to those in Table 1. (Base map provided by Gerard Remolins).

We have organised these samples in 10 different groups (Table 1): 1) Hunter-Gatherers (conformed by Upper Palaeolithic and Mesolithic samples from all around the Peninsula); 2) Early and Middle-Neolithic samples from Navarre; 3) Early and Middle Neolithic from Catalonia (conformed by individuals from sites nearby coasts inhumated in pit graves); 4) Middle-Neolithic Pyr (conformed by individuals buried in stone cists from the Pre-Pyrenean area of Solsonia and the Andorran Pyrenean samples); 5) Middle-Neolithic Midi/Languedoc (conformed by individuals from Midi-Pyrenées and Langedoc regions of France related to the Chasséen culture); 6) Megaliths (those from the Cantabrian fringe in the Basque country); 7) Pico Ramos (Chalcolithic site from the Cantabrian fringe in the Basque Country); 8) Catalan Chalcolithic (Conformed by samples to the south from Barcelona: Can Sadurní and Cova del Pantà de Foix); 9) Roaix (Late-Neolithic site from Provence in France); and 10) Bronze Age Iberian Peninsula (samples from west to east from the south of the Pyreneans).

The analysis of the teeth was carried out following the Arizona State University's Dental Anthropology System (ASUDAS) (Turner et al., 1991), which considers 35 nonmetric dental traits. In individuals with full dentition, these 35 traits provide 121 variables for individual. Most traits are not just present or absent, but ranked in a scale of expression, and the level at which they are represented in each of the antimers of an individual may vary. For this reason, the antimere showing the highest level of expression, which is believed to be the one representing the trait's maximum potential for the individual and be genetically more reliable, is selected in each individual (Turner et al., 1991).

This step is necessary to edit the database before calculating the biological distances, as one of the traits of the correlated pair was eliminated in order to avoid differential weighting of the underlying dimensions that might yield erroneous results (Irish, 2010, Sjøvold, 1977).

The ranked ASUDAS values were later dichotomised into presence or absence values, based on their reported morphological thresholds (Nichol, 1989; Scott, 1973) and according to standard procedure (Irish, 1993; Turner, 1985; 1987). From these dichotomised data, frequencies for the expression of traits were calculated for the different samples and groups. Together with one trait from each pair of correlated traits, those traits that did not present frequency differences in the various samples were excluded from further analysis, because they were non-informative. The correlated traits in our samples were:

The Mean Measure of Divergence (MMD) (Smith, 1972) was calculated between samples as an among-samples phenetic dissimilarity measure. The formula used to calculate the MMD contains Freeman and Tukey's angular transformation to correct for low or high trait frequencies and small sample sizes (Harris & Sjøvold, 2004). Nevertheless, each trait used must have been scored at least 10 times (including present and absent) in each of the compared samples. In order to determine if two samples are significantly different, the MMD has to be compared to its standard deviation (SD). Therefore, if MMD>2xSD, the null hypothesis of P1=P2 is rejected at the 0.025 level. In some cases, when the internal variability of a sample resulted greater to that between the two samples compared negative MMD values might result. These values are statistical artefacts, and therefore, they were set to 0 (Vargiu et al., 2009; Irish, 2010).

Table 1. List of samples included in the study. Minimum number of Individuals (MNI) and number of teeth are provided, as well as the group each of them belongs to.

Site	Group	Name	Chronology/Date	Type of site	Geographical area	References	NMI	Number of teeth
1	H-G	Santimamiñe	Magdalenian	Cave	Biscay	Herrasti & Etxebarria, 2011; López-Quintana & Guenaga-Lizas	1	2
2	H-G	Santa Catalina	11,212-10,851 cal BCE	Cave	Biscay	Albisu *et al.*, 2014; Berganza-Gochi & Arribas-Pastor,2014	1	1
3	H-G	Erralla	Magdalenian	Cave	Gipuzkoa	Altuna *et al.*, 1985	1	2
4	H-G	Balma Guilànya	11,811-10,877 cal BCE	Rock-Sheltter	Lleida	Subirà *et al.*, 2009 a	3	10
5	H-G	Cingle de l'Aigua	10,711-10,211 cal BCE	Rock-Sheltter	Castellón	Román-Monroig, 2010	1	2
6	H-G	La Braña	5,990-5,740 cal BCE; 6,010-5,800 cal BCE	Cave	Leon	Vidal-Encinas & Prada-Marcos,, 2010; Prada-Marcos, 2010	2	35
7	H-G	J3	7530-7180 cal BCE	Rock-Sheltter	Basque Country	Iriarte *et al.*, 2010	1	2
8	H-G	Cingle del Mas Nou	8007–7583 cal BP	Rock-Sheltter	Castellón	Olaria, 2010	2	15
9	H-G	El Collado	7,539-7,356 cal BCE - 6,642-6,486 cal BCE	Rock-Sheltter	Valencia	Campillo *et al.*, 2008; Gibaja *et al.*, 2015	15	73
10	H-G	Casa Corona	8007–7583 cal BP	Open-Air	Alicante	Fernández-López de Pablo *et al.*, 2013	3	20
11	H-G	Moita do Sebastiao	6,200- 5,450 cal BCE	Rock-Sheltter	Muge Estuary (Portugal)	Jackes & Meiklejohn, 2008; Peyroteo-Stjerna, 2016	85	627
12	H-G	Cabeço da Arruda	6,100-4,900 cal BCE	Rock-Sheltter	Muge Estuary (Portugal)	Cunha & Cardoso, 2002-03; Roksandic, 2006; Peyroteo-Stjern	110	382
13	H-G	Cabeço da Amoreira	6,050-5,200 cal BCE	Rock-Sheltter	Muge Estuary (Portugal)	Bicho *et al*., 2013; Cunha & Cardoso, 2001; Roksandic, 2006;	29	37
14	H-G	Arapouco	6,232-5,713 cal BCE	Rock-Sheltter	Sado Estuary (Portugal)	Cunha & Umbelino, 1995-97; Peyroteo-Stjerna, 2016	32-36	15
15	H-G	Cabeço das Amoreiras	6,100-5,300 cal BCE	Rock-Sheltter	Sado Estuary (Portugal)	Cunha & Umbelino, 1995-97; Peyroteo-Stjerna, 2016	6	26
16	H-G	Cabeço do Pez	5,800-5,400 cal BCE	Rock-Sheltter	Sado Estuary (Portugal)	Cunha & Umbelino, 1995-97; Peyroteo-Stjerna, 2016	32	83
17	EN Nav	Los Cascajos	5,140-3,880 cal BCE	Open-Air	Navarre	García & Sesma, 2001; García & Sesma, 2007; García-Gazolaz	27	394
18	EN Nav	Paternanbidea	5,000-4,850 cal BCE	Open-Air	Navarre	García, 2007	9	105
19	E-MN Cat	Canal dels Avellaners	V-IV millenium cal BCE	Reuse of the chanel	Berguedà	Carreras, 1990, Gibaja *et al.*, 2015	1	13
20	NPyr	Corral de Canudas	initial IV millenium cal BCE	Cist	Berguedà	Gibaja *et al.*, 2015	1	18
21	NPyr	Serrat de les tombes	final IV millenium cal BCE	Cist	Berguedà	Servei d'Arqueologia del Berguedà (comunicació personal)	2	46
22	E-MN Cat	Pla del Riu de les Marcetes	3,781-3,650 cal BCE	Pit Burials	Manresa	Guitart i Perarnau, 1986; Oms *et al.*, 2016	1	28
23	E-MN Cat	Can Gelats	initial IV millenium cal BCE	Pit Burials	Girona	Gibaja *et al.*, 2016	1	29
24	E-MN Cat	Hort d'en Grimau	52750-5270	Pit Burials	Penedès	Mestres, 1988-1989; Oms *et al.*, 2016	3	35
25	E-MN Cat	Pujolet de Moja	3,946-3,656 cal BCE	Pit Burials	Penedès	Mestres *et al.*, 1997; Oms *et al.*, 2016	3	90
26	E-MN Cat	Eix Diagonal	V-IV millenium cal BCE	Pit Burials	Penedès	servei d'arqueologia de Catalunya	11	179
27	E-MN Cat	Mas d'en Boixos	4825-4915 cal BC	Pit Burials	Penedès	Bouso *et al.*, 2004, Oms *et al.*, 2016	5	81
28	E-MN Cat	Can Tintorer	IV millenium cal BCE	Pit Burials	Garraf	Oms *et al.*, 2016; Villalba, 1999; Villar *et al.*, 2011	35	324
29	E-MN Cat	C/ Pi 11	initial IV millenium cal BCE	Pit Burials	Barcelona	Cebrià *et al.*, 2016	2	38
30	E-MN Cat	Plaça de la Vila de Madrid	5,479-5,331 cal BCE	Pit Burial	Barcelona	Pou *et al.*, 2010	1	16
31	E-MN Cat	La Gardunya	4000-3936 cal BCE	Pit Burial	Barcelona	Montes *et al.*, 2014, Velasco, 2016	1	20
32	E-MN Cat	Filmoteca	4000 - 3300/3200 a.C	Pit Burial	Barcelona	Nadal & Castillo, 2010, Ruiz *et al.*, 2010	1	28
33	E-MN Cat	Can Gambus	3800-3495 cal BC	Pit Burials	Vallès	Roig *et a.*,l 2010; Villar *et al.*, 2006	27	420
34	E-MN Cat	Bòbila Madurell	4730-4890 cal BC	Pit Burials	Vallès	Oms *et al.*, 2016	102	1,303
35	E-MN Cat	Camí de Can Grau	V-IV millenium cal BCE	Pit Burial	Vallès	Costa *et al.*, 1982; Martí *et al.*, 1997	36	693
36	E-MN Cat	Can Roqueta Can Revella	final V- initial IV millenium c	Pit Burials	Vallès	Morell *et al.*, in press a	3	45
37	E-MN Cat	Can Vinyals	5130-5220 cal BC	Pit Burial	Vallès	Bouso *et al.*, 2004, Oms *et al.*, 2016	3	66
38	E-MN Cat	Can Soldevilla	V-IV millenium cal BCE	Pit Burial	Vallès	Miquel i Serra & Morral, 1980	1	6
39	NPyr	Segudet	4,323-4,052 cal BCE	Cist	Andorra	Remolins *et al.*, 2016	1	15
40	NPyr	Feixa del Moro	3,978-3,787 cal BCE; 3,946,3	Cist	Andorra	Remolins *et al.*, 2016	1	13
41	NPyr	Can Ignasi	Neolithic	Cist	Solsonès	Fígols, 1996	1	4
42	NPyr	Cementiri de Solsona	Neolithic	Cist	Solsonès	Fígols, 1996	1	9
43	NPyr	Ceuró I, II	3,941-3,666 cal BCE; 3,909-3,657 cal BCE	Cist	Solsonès	Morell *et al.*, in press b	3	46
44	NPyr	Cista de la Puput	Neolithic	Cist	Solsonès	Lorencio C, Xandri J, Canela M. 1983	1	7
45	NPyr	Colilles	Neolithic	Cist	Solsonès		2	24
46	NPyr	Costa dels Garrics del Caballol I, II	3,943-3,638 cal BCE; 3,760-3,526 cal BCE; 3,634-3,375 cal BCE; 3,635-3,376 cal BCE	Cist	Solsonès	Castany, 1991; Morell *et al.*, in press b	3	71
47	NPyr	El Llord I, II, V	3,340-2,575 cal BCE	Cist	Solsonès	Castany, 2009	5	87
48	NPyr	El Megalit del Senyor Bisbe	3,975-3,800 cal BCE	Cist	Solsonès	Morell *et al.*, in press b	1	24
49	NPyr	El Vilar de Simosa	3,931-3,665 cal BC	Cist	Solsonès	Morell *et al.*, in press b	4	99
50	NPyr	Estació del Solar III	3,926-3,661 cal BCE; 3,930-3,664 cal BCE	Cist	Solsonès	Morell *et al.*, in press b	2	23
51	NPyr	Fossa del Camí dels Casals	Neolithic	Cist	Solsonès	Castany i Guerrero 1989	1	6
52	NPyr	Les Censades	Neolithic	Cist	Solsonès	Serra Vilaró, 1927	2	27
53	NPyr	Palà de Coma I, II	3,785-3,364 cal BCE	Cist	Solsonès	Fígols, 1996	3	42
54	NPyr	Cal Tururut	Neolithic	Cist	Solsonès	Castany i Guerrero 1983-84	1	3
55	NPyr	Tomba del Moro de Sorba	3,895-3,655 cal BCE	Cist	Solsonès	Morell *et al.*, in press	2	25
56	NPyr	Boixadera dels Bancs	Neolithic	Sepulchral cave	Solsonès	Serra Vilaró, 1927	16	131
57	NMidiLang	La Terrase, Villeneuve-Tolosane/ La Vimona et Zag Agora, Cugnaux	4,200-3,800 cal BC	Pit Burials	Midi-Pyrenees/Languedoc	Gandelin & Vaquer, 2008	10	183
58	NMidiLang	Narbons	4,248-3,3369 cal BC	Pit Burials	Midi-Pyrenees/Languedoc	Tchéremissinof *et al.*, 2005	3	71
59	NMidiLang	Le Crés	End of V millennium BCE	Pits and Cists	Languedoc-Rousillon	Loison *et al.*, 2004; Loison & Schmitt, 2009	39	467
60		Pico Ramos	3,911-3,346; 3,091-2,486; 2,913-2,347 cal BCE	Sepulchral cave	Biscay	Zapata, 1995	104	2,294
61		Roaix (Couche 5)	End of IV millennium BCE	Hypogeum	Provence	Courtin, 1974; Sauzade, 1983	159	2,994
62	Chal Cat	Can Sadurní (Capa 9)	4135-4315 cal BCE	Sepulchral cave	Garraf	Edo *et al.*, 1982, Oms *et al.*, 2016	50	1,028
63	Chal Cat	Cova del Pantà de Foix	3,420-2,640 cal BCE	Sepulchral cave	Garraf	Cebrià *et al.*, 2013	30	321
64	Megaliths	Argarbi	Chalcolithic	Megalith	Gipuzkoa	Mujika & Edeso, 2012	12	180
65	Megaliths	Gorostiaran Oeste	Chalcolithic	Megalith	Gipuzkoa	Aranzadi *et al.*, 1919; Mujika & Edeso, 2012	4	74
66	Megaliths	Gorostiaran Este	Chalcolithic	Megalith	Gipuzkoa	Aranzadi *et al.*, 1919; Mujika & Edeso, 2012	4	74
67	Bronze	Urtiaga	1,800-1,740 cal BCE	Cave	Gipuzkoa	Altuna & de la Rúa, 1989	25	587
68	Bronze	Iruaxpe I	Bronze Age	Cave	Gipuzkoa	Altuna *et al.*, 1995	15	320
69	Bronze	Pikandita	Bronze Age	Cave	Gipuzkoa	Altuna *et al.*, 1995; Armendariz & Etxeberria, 1983	4	58
70	Bronze	Ceuró III	2,022-1,7778 cal BCE	Cist	Solsonès	López-Onaindia *et al.*, 2017	1	7
71	Bronze	Altaracs I	1,623-1,461 cal BCE	Cist	Solsonès	López-Onaindia *et al.*, 2017	1	8
72	Bronze	Coïns	Bronze Age	Cist	Solsonès	inventari patrimoni arqueològic de la Generalitat	2	9
73	Bronze	Cova de Sant Bartomeu	Bronze Age	Cave	Solsonès	Soriano, 2013	9	36
74	Bronze	Forat de la Tuta	1,739-1,508 cal BCE	Cave	Solsonès	Soriano, 2011	1	5
75	Bronze	Dolmen de Clarà	909-798 cal BCE	megalith	Solsonès	Museu Diocesal i Comarcal de Solsona; Castany, 1991	3	12
76	Bronze	Santes Masses	2,141-1,882 cal BCE	Cist	Solsonès	Castany et al., 1994, inventari Patrimoni Arqueològic de Catal	2	36
77	Bronze	Collet de les Forques	Bronze Age	megalith	Solsonès	Serra Vilaró, 1927	4	40
78	Bronze	La Guàrdia	Bronze Age	Tumulus	Solsonès	Crònica de la Secció Arqueològica. 1915-1920	1	13
79	Bronze	Collet de Saltzer I	Bronze Age	Megalith	Solsonès	Baulenas *et al.*, 2008	2	12
80	Bronze	Aigües Vives	1,880-1,330 cal BCE	Paradolmen	Solsonès	Castany, 1991; Pedro, 2008	9	72
81	Bronze	Els Pinetons	III millenium BCE	Tumulus	Vallès	Balsera *et al.*, 2010	40	279
							1,184-1,188	15,145

al., 2001). This representation is useful to obtain further information beyond if two samples are significantly different or not. The representations offer a stress value that indicates the accuracy with which the matrix has been represented. Usually, stress values <0.10 are considered excellent, and ≥0.15 unacceptable (Borgatti, 1997). Moreover, a Principal Component Analysis (PCA) was also carried out with PAST based on the same traits used to calculate the MMD. This analysis usually provides complementary information on which traits are more involved in the distribution observed on the MDS representation.

Results

Sample size, presence values and frequencies for the analysed traits in all groups are provided in Table 2. In order to maximize sample size for the later analyses, from the correlated traits, those that were scored in fewer individuals were excluded from the posterior steps. Based on the trait frequencies, it was observed that all the samples present the ratios into the Eurodont morphological complex for Western Europe.

15 traits were used to calculate the MMD distances after excluding one of each correlated trait, and also those traits that did not show differences between groups and, therefore, where not discriminative. The matrix obtained with all these distances (Table 3) showed that the only two samples that did not show significant differences with the Hunter-Gatherer sample were the Early-Neolithic one from Navarre and the Bronze-Age group. In the opposite sense, the farmer group that diverged most from the Pre-Neolithic one was the Megalithic sample. On the other hand, the French Middle-Neolithic sample was the one that diverges most from the Early-Neolithic Iberian and the Catalan coastal samples. In addition, the sample of Roaix was less divergent from Pico Ramos, Iberian Bronze Age, and Hunter-Gatherers, than from the French Neolithic or Coastal Iberian Chalcolithic samples.

In order to obtain a more reliable representation, we excluded Roaix from the MDS. The representation (Figure 2) showed a central group formed by the Hunter-Gatherers, Early-Neolithic sample from Navarre, and the Bronze Age sample from the Peninsula. Separated from this core, two groups were observed: on one hand the Early- and Middle-Neolithic from the coastal areas of the Northeast of the Peninsula, and the Megalithic samples from the Cantabrian Fringe. On the other hand, the Middle-Neolithic Iberian group from the Pre-Pyreneans and Pyreneans, and the French Middle-Neolithic sample from Midi-Pyrenees and Languedoc area.

The PCA analysis showed a similar representation compared to the MDS, and that the combination of the first two components explained 65.4% of the total variation on the sample. The correlation values between traits and components, indicate that the main traits responsible for the dispersion of the samples were: *UI1 Shovelling*, *UM1 Hypocone*, *UM1 Carabelli*, *UM2 Cusp5*, *LP4 Lingual cusps*, *LM1 Cusp5*, and *LM1 Cusp 6* (Table 4). Concretely, in the separation observed along the horizontal axis, we observed that the Sepulcres de Fossa and Megalithic samples presented more elevated frequencies for *UM2 Cusp5* and *LP4 Lingual cusp*, while the Midi Pyrenees-Languedoc sample presented higher ratios for *UI2 Shovelling* and *LM1 Cusp5*. The vertical axis separated the Middle-Neolithic samples together with the Megaliths and Catalan Chalcolithic sample in the positive area; and Hunter-Gatherers, Early Neolithic from Navarre, Pico Ramos and Bronze Age samples in the negative. These differences could be explained due to the higher presence ratios of *LM1 Cusp6* among those samples in the positive area, and higher ratios of *UM1 Hypocone* and *UM1 Carabelli* among those in the negative zone.

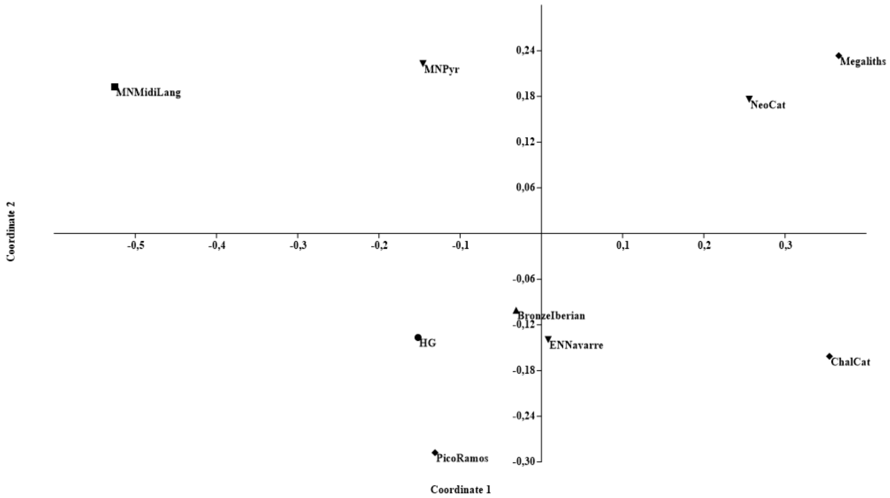

Figure 2. MDS representation of the MMD distance matrix. The stress value associated to this representation was 0.138. HG: Hunter-Gatherers; Neo Cat: Early- and Middle-Neolithic samples related to Sepulcres de Fossa Culture; MNPyr: Middle Neolithic from Solsonian and Andorran areas; MNMidiLang: Middle Neolithic from Midi-Pyrennées and Langedoc areas; ChalCat: Chalcolithic from Catalan coastal areas.

Table 2.1 Sample sizes, presence recount, frequencies, and dichotomic breaking points for the studied maxillary traits in the studied samples.

		Hunter Gatherers			EN Navarre			EN-MN Catalonia			NM Pyr			MN Midi Pyr-Languedoc			Pico Ramos			Roaix			Chalco Litoral			Megaliths			ronze Age Iberian Peninsul		
Trait	**Breaking point**	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq
I1 Labial curve	1/1-4	22	1	0.045455				46	26	0.565217	16	4	0.25	1	0	0	66	19	0.287879	88	35	0.397727	50	19	0.38				15	2	0.133333
I1 Interrup. Groove	1/0-1	29	2	0.068966	19	1	0.052632	63	12	0.190476	8	0	0	27	6	0.222222	88	8	0.090909	115	13	0.113043	61	13	0.213115	26	4	0.153846	59	5	0.084746
I1 Shovel	3-6/0-6	19	3	0.157895	19	2	0.105263	61	8	0.131148	15	1	0.066667	25	11	0.44	71	7	0.098592	67	7	0.104478	47	4	0.085106	17	0	0	47	4	0.085106
I1 Double shovel	2-6/0-6	28	3	0.107143	21	0	0	76	4	0.052632	17	1	0.058824	26	0	0	78	3	0.038462	106	4	0.037736	54	1	0.018519	23	1	0.043478	53	1	0.018868
I1 I&C t.d.	2-6/0-6	10	2	0.2	20	0	0	67	11	0.164179	13	4	0.307692	26	5	0.192308	54	12	0.222222	50	14	0.28	64	9	0.140625	26	1	0.038462	55	11	0.2
I2 Interrup. Groove	1/0-1	40	8	0.2	15	6	0.4	85	35	0.411765	3	1	0.333333	30	7	0.233333	96	16	0.166667	113	17	0.150442	91	26	0.285714	25	7	0.28	56	13	0.232143
I2 Shovel	3-7/0-7	26	9	0.346154	15	4	0.266667	78	10	0.128205	13	5	0.384615	25	13	0.52	89	20	0.224719	75	34	0.453333	81	9	0.111111	23	1	0.043478	51	14	0.27451
I2 Double shovel	2-6/0-6	36	7	0.194444	17	0	0	83	6	0.072289	16	2	0.125	23	1	0.043478	97	0	0	108	3	0.027778	73	4	0.054795	25	2	0.08	51	1	0.019608
I2 I&C t.d.	2-6/0-6	20	2	0.1	14	1	0.071429	81	20	0.246914	14	3	0.214286	25	6	0.24	77	16	0.207792	52	9	0.173077	96	20	0.208333	25	10	0.4	54	9	0.166667
I2 Root nº	2/1-2	5	0	0	0	0		20	16	0.8	14	0	0	2	2	1	85	85	1	95	95	1	93	0	0				27	17	0.62963
I2 Peg (<7)/reduce	2/0-2	54	0	0	16	0	0	58	2	0.034483	18	0	0	4	0	0	101	1	0.009901	107	0	0	13	1	0.076923	26	2	0.076923	47	0	0
I2 cong absence	1/0-1	4	0	0	17	0	0	89	4	0.044944	26	0	0	7	0	0	5	1	0.2	14	1	0.071429				17	0	0	39	0	0
C I&C t.d.	2-6/0-6	30	15	0.5	22	0	0	94	19	0.202128	22	1	0.045455	25	6	0.24	46	25	0.543478	65	22	0.338462	73	8	0.109589	15	2	0.133333	64	9	0.140625
C mesial ridge	2-5/0-5	29	6	0.206897	21	6	0.285714	79	23	0.291139	18	3	0.166667	18	0	0	56	3	0.053571	71	0	0	58	6	0.103448	14	5	0.357143	55	12	0.218182
C Dist. access ridge	2-5/0-5	23	4	0.173913	20	2	0.1	74	30	0.405405	18	8	0.444444	18	2	0.111111	50	12	0.24	66	30	0.454545	42	10	0.238095	13	5	0.384615	51	13	0.254902
C Root nº	1/1-2	7	1	0.142857	22	22	1	53	47	0.886792	13	0	0	0	0		67	67	1	109	109	1	63	63	1	14	17	1.214286	62	53	0.854839
P3 Double shovelling	2-6/0-6	43	6	0.139535	17	1	0.058824	60	3	0.05				3	0	0	46	3	0.065217	95	11	0.115789				15	6	0.4	44	7	0.159091
P3 m&d cusps	1/0-1	40	3	0.075	13	1	0.076923	90	13	0.144444	21	0	0	1	0	0	63	4	0.063492	77	0	0	49	4	0.081633	15	4	0.266667	53	6	0.113208
P3 Enamel ext.	1-3/0-3	6	1	0.166667	15	3	0.2	71	6	0.084507	23	0	0	3	0	0	60	0	0	90	3	0.033333	38	1	0.026316	15	0	0	59	0	0
P3 Root nº	1/1-2	4	2	0.5	14	4	0.285714	52	32	0.615385	10	2	0.2	17	10	0.588235	46	16	0.347826	59	27	0.457627	38	15	0.394737	9	7	0.777778	51	27	0.529412
P3 Odontome	1/0-1	1	0	0	14	0	0	62	1	0.016129				22	0	0	56	1	0.017857	70	0	0				15	0	0	13	0	0
P4 m&d cusps	1/0-1	37	1	0.027027	17	3	0.176471	76	6	0.078947	22	1	0.045455	3	0	0	87	3	0.034483	119	2	0.016807	51	2	0.039216	13	2	0.153846	42	3	0.071429
P4 Enamel ext.	1-3/0-3	64	1	0.015625	21	0	0	66	1	0.015152	23	0	0	1	0	0	91	0	0	146	1	0.006849	41	0	0	20	0	0	52	0	0
P4 Root nº	1/1-2	4	0	0	17	17	1	47	42	0.893617	9	0	0	11	10	0.909091	69	68	0.985507	108	108	1	50	46	0.92	18	16	0.888889	50	39	0.78
P4 Odontome	1/0-1	1	0	0	19	0	0	57	0	0				18	0	0	84	0	0	103	1	0.009709	61	0	0	21	0	0	24	0	0
P4 Congenital Absence	1/0-1	1	0	0	24	0	0	76	0	0				7	0	0	110	0	0	34	0	0							7	0	0
M1 Metacone	2-5/0-5	78	78	1	27	27	1	112	106	0.946429	27	27	1	7	7	1	86	86	1	105	105	1	64	64	1	15	15	1	53	53	1
M1 Hypocone	2-5/0-5	76	76	1	27	27	1	110	103	0.936364	26	25	0.961538	39	38	0.974359	86	86	1	101	101	1	62	60	0.967742	11	11	1	55	55	1
M1 Cusp 5	1-5/0-5	64	5	0.078125	21	0	0	107	20	0.186916	28	0	0	23	1	0.043478	75	3	0.04	90	1	0.011111	56	16	0.285714	12	1	0.083333	53	5	0.09434
M1 Carabelli	2-7/0-7	37	9	0.243243	14	4	0.285714	86	15	0.174419	21	3	0.142857	36	4	0.111111	50	22	0.44	49	23	0.469388	46	11	0.23913	10	1	0.1	39	11	0.282051
M1 C2 parastyle	1-5/0-5	58	1	0.017241	28	0	0	98	7	0.071429	27	3	0.111111	38	0	0	69	0	0	87	0	0	47	4	0.085106	14	1	0.071429	47	2	0.042553
M1 Enamel ext.	1-3/0-3	4	1	0.25	26	2	0.076923	86	11	0.127907	27	0	0	35	2	0.057143	58	3	0.051724	81	6	0.074074	46	6	0.130435	12	2	0.166667	50	8	0.16
M1 Root nº	3/1-3	5	3	0.6	27	27	1	68	53	0.779412	11	10	0.909091	3	3	1	60	58	0.966667	46	44	0.956522	55	51	0.927273	17	17	1	37	35	0.945946
M2 Metacone	2-5/0-5	72	72	1	27	27	1	101	93	0.920792	29	29	1	10	10	1	85	85	1	119	118	0.991597	52	51	0.980769	18	18	1	65	65	1
M2 Hypocone	2-5/0-5	63	55	0.873016	27	24	0.888889	99	76	0.767677	29	20	0.689655	31	22	0.709677	70	48	0.685714	107	74	0.691589	43	38	0.883721	17	14	0.823529	63	50	0.793651
M2 Cusp 5	1-5/0-5	66	7	0.106061	27	4	0.148148	99	16	0.161616	29	2	0.068966	24	3	0.125	60	10	0.166667	101	10	0.09901	42	7	0.166667	18	6	0.333333	62	9	0.145161
M2 Carabelli	2-7/0-7	49	2	0.040816	24	1	0.041667	94	7	0.074468	27	1	0.037037	25	1	0.04	42	0	0	60	3	0.05	38	2	0.052632	16	0	0	50	1	0.02
M2 C2 parastyle	1-5/0-5	68	4	0.058824	27	1	0.037037	95	8	0.084211	29	2	0.068966	32	0	0	75	1	0.013333	105	3	0.028571	43	1	0.023256	15	3	0.2	56	2	0.035714
M2 Enamel ext.	1-3/0-3	5	1	0.2	24	1	0.041667	80	11	0.1375	28	0	0	30	1	0.033333	74	4	0.054054	92	5	0.054348	41	7	0.170732	8	2	0.25	60	9	0.15
M2 Root nº	3/1-3	4	1	0.25	20	17	0.85	61	41	0.672131	14	10	0.714286	4	2	0.5	60	39	0.65	63	48	0.761905	46	32	0.695652	13	11	0.846154	56	33	0.589286
M3 Metacone	2-5/0-5	50	49	0.98	17	17	1	75	69	0.92	18	18	1	7	7	1	65	65	1	92	88	0.956522	34	34	1	15	15	1	48	48	1
M3 Hypocone	2-5/0-5	53	27	0.509434	17	9	0.529412	73	28	0.383562	18	10	0.555556	7	0	0	57	23	0.403509	89	42	0.47191	33	17	0.515152	15	4	0.266667	48	23	0.479167
M3 Cusp 5	1-5/0-5	51	12	0.235294	17	2	0.117647	74	14	0.189189	18	4	0.222222	6	1	0.166667	56	22	0.392857	88	36	0.409091	34	8	0.235294	14	5	0.357143	45	12	0.266667
M3 Carabelli	2-7/0-7	43	2	0.046512	16	0	0	70	8	0.114286	17	0	0	2	0	0	48	6	0.125	63	0	0	33	1	0.030303	13	1	0.076923	40	2	0.05
M3 C2 parastyle	1-5/0-5	41	3	0.073171	17	1	0.058824	69	11	0.15942	18	1	0.055556	7	0	0	61	1	0.016393	87	2	0.022989	33	2	0.060606	15	1	0.066667	41	4	0.097561
M3 Enamel ext.	1-3/0-3	6	0	0	15	0	0	57	9	0.157895	17	0	0	8	1	0.125	55	4	0.072727	72	6	0.083333	31	2	0.064516	11	4	0.363636	34	4	0.117647
M3 Root nº	3/1-3	2	0	0	12	7	0.583333	38	9	0.236842				5	0	0	38	8	0.210526	43	6	0.139535	20	6	0.3	12	0	0	24	1	0.041667
M3 Peg (<7)/reduce	2/0-2	5	0	0	15	0	0	53	4	0.075472	18	0	0	7	0	0	64	0	0	87	1	0.011494	34	3	0.088235	13	0	0	32	0	0
M3 cong. Absence	1/0-1	55	0	0	17	0	0	63	0	0	20	1	0.05	9	0	0	67	0	0	27	0	0	37	0	0	10	0	0	11	0	0

Table 2.2. . Sample sizes, presence recount, frequencies, and dichotomic breaking points for the mandibular traits in the studied samples.

		Hunter Gatherers			EN Navarre			EN-MN Catalonia			NM Pyr			MN Midi Pyr-Languedoc			Pico Ramos			Roaix			Chalco Litoral			Megaliths			ronze Age Iberian Peninsul		
Trait	**Breaking point**	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq	N	Presence	Freq
I1 Shovelling	2-3/0-3	34	0	0	14	0	0	66	3	0.045455	15	0	0	22	0	0	64	0	0	90	0	0	45	1	0.022222	16	0	0	46	0	0
I1 Double shovelling	2-6/0-6	31	2	0.064516	14	0	0	72	3	0.041667				2	0	0	80	1	0.0125	104	2	0.019231	52	2	0.038462	16	3	0.1875	38	0	0
I1 Congenital Absence	1/0-1	49	0	0	15	0	0	59	1	0.016949				5	0	0	124	0	0	34	0	0				22	0	0	45	0	0
I2 Shovel	2-3/0-3	45	1	0.022222	16	1	0.0625	78	7	0.089744	19	0	0	28	0	0	91	5	0.054945	89	4	0.044944	64	7	0.109375	13	1	0.076923	57	3	0.052632
I2 Double Shovelling	2-6/0-6	38	1	0.026316	17	1	0.058824	82	10	0.121951	1	0	0	5	0	0	100	1	0.01	96	2	0.020833	55	10	0.181818	12	3	0.25	54	1	0.018519
C Dist. access ridge	2-5/0-5	29	5	0.172414	18	0	0	66	19	0.287879	21	5	0.238095	14	1	0.071429	47	7	0.148936	61	5	0.081967	39	7	0.179487	10	0	0	38	3	0.078947
C Root nº	1/1-2	3	0	0	16	13	0.8125	64	52	0.8125	16	2	0.125	20	16	0.8	61	58	0.95082	61	61	1	63	56	0.888889	16	15	0.9375	61	47	0.770492
P3 lingual cusps	2-9/0-9	41	13	0.317073				56	31	0.553571	24	4	0.166667	28	6	0.214286	106	16	0.150943	148	35	0.236486	70	25	0.357143				43	14	0.325581
P3 Enamel ext.	1/0-1	2	0	0	15	0	0	65	3	0.046154	28	0	0	6	0	0	111	2	0.018018	173	0	0	58	1	0.017241	18	0	0	83	1	0.012048
P3 Root nº	1/1-2	2	0	0	13	13	1	59	49	0.830508	12	0	0	16	15	0.9375	83	82	0.987952	128	127	0.992188	54	30	0.555556	16	16	1	75	64	0.853333
P3 Odontome	1/0-1	0	0		19	0	0	83	3	0.036145				24	0	0	107	0	0	136	1	0.007353	60	0	0				50	0	0
P4 lingual cusps	2-9/0-9	38	20	0.526316	18	13	0.722222	82	53	0.646341	21	9	0.428571	17	4	0.235294	90	60	0.666667	117	77	0.65812	48	20	0.416667	16	14	0.875	57	42	0.736842
P4 Enamel ext.	1/0-1	3	0	0	18	0	0	65	4	0.061538	26	0	0	7	0	0	109	0	0	133	0	0	61	1	0.016393	19	0	0	69	1	0.014493
P4 Root nº	1/1-2	3	0	0	13	13	1	55	43	0.781818	9	0	0	2	2	1	93	93	1	98	98	1	70	69	0.985714	18	18	1	57	48	0.842105
P4 Odontome	1/0-1	2	0	0	18	0	0	32	3	0.09375				18	0	0	99	0	0	107	0	0	52	0	0	14	0	0	39	0	0
P4 Congenital Absence	1/0-1	75	0	0	23	0	0	86	0	0				7	0	0	137	1	0.007299	59	0	0	66	0	0	21	0	0	8	0	0
M1 Groove pattern	Y/Y,+,X	34	19	0.558824	8	7	0.875	48	35	0.729167	24	21	0.875	4	4	1	68	51	0.75	89	77	0.865169	57	25	0.438596	9	7	0.777778	41	34	0.829268
M1 Cusp nº	6-7/4-7	74	1	0.013514	22	1	0.045455	96	6	0.0625	33	3	0.090909	4	0	0	88	4	0.045455	127	6	0.047244	86	14	0.162791	16	4	0.25	71	3	0.042254
M1 Def Wrinkle	2-3/0-3	18	7	0.388889	3	1	0.333333	50	11	0.22	13	0	0	2	0	0	26	1	0.038462	14	0	0	33	5	0.151515	12	5	0.416667	28	3	0.107143
M1 Distal crest	1/0-1	22	0	0	5	0	0	61	8	0.131148	12	1	0.083333	2	0	0	59	0	0	45	0	0	60	1	0.016667	15	0	0	28	1	0.035714
M1 Protostylid	2-7/0-7	55	2	0.036364	14	1	0.071429	89	9	0.101124	32	0	0	2	0	0	68	0	0	73	0	0	59	0	0	17	3	0.176471	58	6	0.103448
M1 Cusp 5	3-5/0-5	71	53	0.746479	22	10	0.454545	100	52	0.52	32	18	0.5625	28	26	0.928571	87	71	0.816092	128	112	0.875	89	53	0.595506	16	8	0.5	71	58	0.816901
M1 Cusp 6	2-5/0-5	69	0	0	22	0	0	99	6	0.060606	32	2	0.0625	26	1	0.038462	84	0	0	125	1	0.008	83	4	0.048193	15	2	0.133333	69	1	0.014493
M1 Cusp 7	1-4/0-4	77	0	0	22	0	0	103	12	0.116505	35	1	0.028571	28	3	0.107143	95	1	0.010526	130	1	0.007692	88	1	0.011364	17	0	0	67	3	0.044776
M1 Enamel ext.	1-3/0-3	3	0	0	21	3	0.142857	82	9	0.109756	34	0	0	7	0	0	90	10	0.111111	117	4	0.034188	69	5	0.072464	23	7	0.304348	62	8	0.129032
M1 Root nº	3/1-3	2	0	0	16	0	0	65	0	0	14	0	0	18	0	0	80	2	0.025	70	1	0.014286	100	1	0.01	20	0	0	34	0	0
M2 Groove pattern	Y/Y,+,X	65	16	0.246154	20	2	0.1	85	12	0.141176	32	9	0.28125	21	2	0.095238	109	15	0.137615	121	11	0.090909	47	4	0.085106	12	4	0.333333	64	11	0.171875
M2 Cusp nº	4/4-6	81	79	0.975309	24	20	0.833333	109	88	0.807339	34	34	1	6	6	1	140	127	0.907143	165	135	0.818182	73	55	0.753425	15	11	0.733333	76	69	0.907895
M2 Def Wrinkle	2-3/0-3	26	6	0.230769	9	2	0.222222	67	17	0.253731	25	0	0	0	0		44	2	0.045455	19	0	0	43	7	0.162791	13	7	0.538462	46	4	0.086957
M2 Distal crest	1/0-1	47	2	0.042553	18	1	0.055556	86	8	0.093023	24	3	0.125	0	0		103	1	0.009709	108	0	0	53	2	0.037736	18	1	0.055556	59	14	0.237288
M2 Protostylid	2-7/0-7	59	1	0.016949	21	1	0.047619	103	7	0.067961	34	6	0.176471	1	0	0	84	4	0.047619	102	1	0.009804	56	0	0	18	1	0.055556	68	8	0.117647
M2 Cusp 5	3-5/0-5	78	5	0.064103	24	2	0.083333	110	8	0.072727	34	2	0.058824	28	4	0.142857	143	3	0.020979	161	5	0.031056	73	8	0.109589	15	2	0.133333	75	3	0.04
M2 Cusp 6	3-5/0-5	80	1	0.0125	24	0	0	110	5	0.045455	35	0	0	6	0	0	143	0	0	163	1	0.006135	75	1	0.013333	15	0	0	74	0	0
M2 Cusp 7	1-4/0-4	79	0	0	24	0	0	112	7	0.0625	36	2	0.055556	28	3	0.107143	147	0	0	164	1	0.006098	76	0	0	18	0	0	74	0	0
M2 Enamel ext.	1-3/0-3	2	0	0	22	3	0.136364	89	19	0.213483	34	2	0.058824	8	0	0	129	18	0.139535	139	10	0.071942	51	13	0.254902	15	3	0.2	73	19	0.260274
M2 Root nº	1/1-3	1	0	0	12	0	0	66	5	0.075758	16	0	0	2	1	0.5	98	15	0.153061	76	15	0.197368	76	10	0.131579	16	2	0.125	46	1	0.021739
M3 Groove pattern	Y/Y,+,X	44	21	0.477273	13	5	0.384615	59	14	0.237288	27	7	0.259259	4	1	0.25	61	14	0.229508	78	11	0.141026	21	9	0.428571	7	2	0.285714	44	18	0.409091
M3 Cusp nº	4/4-6	55	42	0.763636	15	10	0.666667	85	36	0.423529	30	29	0.966667	8	5	0.625	71	28	0.394366	88	36	0.409091	30	16	0.533333	8	5	0.625	55	42	0.763636
M3 Def Wrinkle	2-3/0-3	16	5	0.3125	7	0	0	59	18	0.305085	23	1	0.043478				26	1	0.038462	17	1	0.058824	15	5	0.333333	6	3	0.5	33	6	0.181818
M3 Distal crest	1/0-1	36	3	0.083333	12	1	0.083333	73	11	0.150685	19	2	0.105263	3	0	0	50	3	0.06	66	1	0.015152	24	12	0.5	8	0	0	38	11	0.289474
M3 Protostylid	2-7/0-7	47	3	0.06383	14	0	0	79	11	0.139241	28	6	0.214286	3	0	0	53	6	0.113208	73	7	0.09589	27	1	0.037037	8	1	0.125	43	10	0.232558
M3 Cusp 5	3-5/0-5	55	13	0.236364	15	3	0.2	86	23	0.267442	31	16	0.516129	7	1	0.142857	70	31	0.442857	89	43	0.483146	31	8	0.258065	8	1	0.125	53	21	0.396226
M3 Cusp 6	2-5/0-5	55	2	0.036364	15	1	0.066667	84	9	0.107143	31	2	0.064516	8	0	0	69	5	0.072464	96	5	0.052083	30	0	0	8	2	0.25	53	2	0.037736
M3 Cusp 7	1-4/0-4	55	0	0	15	0	0	84	8	0.095238	29	1	0.034483	7	0	0	71	1	0.014085	97	2	0.020619	31	0	0	8	1	0.125	49	1	0.020408
M3 Enamel ext.	1-3/0-3	1	0	0	13	0	0	69	7	0.101449	28	0	0	9	0	0	61	5	0.081967	73	5	0.068493	16	4	0.25	5	2	0.4	42	5	0.119048
M3 Root nº	3/1-3	1	0	0	4	0	0	45	4	0.088889	15	1	0.066667	2	0	0	45	2	0.044444	35	0	0	21	0	0	8	1	0.125	28	0	0
M3 Torsomolar angle	1/0-1	35	2	0.057143	12	4	0.333333	65	3	0.046154	21	4	0.190476	7	0	0	20	4	0.2	42	0	0				1	1	1	17	3	0.176471
M3 Cong. Absence	1/0-1	54	0	0	15	0	0	85	7	0.082353	39	1	0.025641	9	0	0	76	0	0	57	0	0	32	0	0	4	0	0	27	3	0.111111

Table 3. Distance values between the analysed samples (above diagonal) and the standard deviation for each distance calculation (below diagonal). The statistically significant distances are shown in bold.

	HG	ENNavarre	NeoCat	MNPyr	MNMidiLang	PicoRamos	Roaix	ChalCat	Megaliths	BronzeIberian
HG	-	-0.0084117	**0.09724718**	**0.03321917**	**0.06500456**	**0.02204848**	**0.05689837**	**0.05653477**	**0.12799576**	-0.0012867
ENNavarre	0.00026789	-	**0.06707876**	**0.04930995**	**0.1439975**	**0.02577084**	**0.08225438**	**0.05502829**	**0.07157134**	0.01081201
NeoCat	6.4331E-05	0.00016794	-	**0.05108308**	**0.16414173**	**0.09780375**	**0.15922814**	**0.02560887**	**0.01033384**	**0.0488657**
MNPyr	0.00025076	0.00042971	0.00015192	-	**0.05257411**	**0.07799585**	**0.07169501**	**0.10212885**	**0.08701526**	**0.0530701**
MNMidiLang	0.0001751	0.00032806	9.739E-05	0.00030686	-	**0.12426126**	**0.13007619**	**0.13535801**	**0.269889**	**0.08868973**
PicoRamos	7.4013E-05	0.00018379	2.7023E-05	0.00016584	0.00011079	-	**0.01501676**	**0.09639432**	**0.12255698**	-0.0058993
Roaix	7.2399E-05	0.00018062	2.4839E-05	0.00016298	0.00010528	3.2071E-05	-	**0.17564924**	**0.21478399**	**0.02933473**
ChalCat	8.4562E-05	0.00020165	3.5422E-05	0.0001825	0.0001269	4.4787E-05	4.0473E-05	-	**0.06918441**	**0.0629498**
Megaliths	0.00036041	0.00058442	0.00025832	0.00054376	0.00044772	0.00028153	0.00027202	0.00030768	-	**0.0697897**
BronzeIberian	8.8696E-05	0.00020871	3.6348E-05	0.0001893	0.00012798	4.5055E-05	4.2211E-05	5.5519E-05	0	-

Table 4. Correlations between traits and the first to Principal Components for the analysis regarding the same samples as the MMD and MDS. The first component represents 46.81% of the variability and the second 18.64%.

	PC1 (46.81%)	PC2 (18.64%)
UI2 Shovelling	-0.8981	0.01958
UI2 Tuberculum dentale	0.4091	0.6063
UC Distal Accessory Ridge	0.5421	0.6206
UM1 Hypocone	0.06745	-0.7085
UM1 Cusp5	0.2269	0.2147
UM1 Carabelli's tubercle	-0.02679	-0.8404
UM2 Hypocone	0.364	-0.2943
UM2 Cusp5	0.7297	0.03091
LI2 Shovelling	0.6941	-0.1426
LP4 Lingual cusps	0.8512	-0.4212
LM1 Cusp5	-0.758	-0.2485
LM1 Cusp6	0.5379	0.7451
LM1 Cusp7	-0.3562	0.4006
LM2 Groove pattern	0.4271	0.3567
LM2 Cusp5	-0.02487	0.5197

Discussion

Modern humans have continuously inhabited the Iberian Peninsula since the Middle Palaeolihtic and until the current day. This includes the Last Glacial Maximum, period when, according to different evidences, the Peninsula was one of the refuges in Europe (Gamble et al., 2005; Garate et al., 2014, 2015). In previous studies we have observed that the Mesolithic population from the Iberian Peninsula was biologically different from the Italian sample (López-Onaindia et al., submitted a). These results have also been reported in aDNA studies, which found that the mitochondrial haplogroups present in Iberian Hunter-Gatherer populations differed from those found in Central Europe (de la Rúa et al., 2015; Hervella et al., 2012; Szécsény-Nagy et al., 2017).

The current results indicate that populations with different biological origin coexisted in the Northeast of the Iberian Peninsula during Early- and Middle-Neolithic. Concretely, we have observed that there is a group that stands close to the Pre-Neolithic sample, the group from Navarre (Upper-Ebro Valley); while two samples differ from the Hunter-Gatherer sample, the Mediterranean coastal sample, and the sample corresponding to mountainous groups. Previous results also pointed out that the group identified by the funerary culture of Sepulcres de Fossa (Mediterranean coastal) is the one that diverges most from the Pre-Neolithic sample (López-Onaindia et al., submitted a). Nevertheless, each of these two groups presented larger differences comparing to the Italian Hunter-Gatherer and Neolithic samples, than between each other.

Moreover, although the Sepulcpres de Fossa group and the Solsonian group were different, in this case both were more similar between each other than they were regarding the Italian samples (López-Onaindia et al., *in press*). In this sense, when the sample of Los Cascajos (Early- and Middle-Neolithic Navarre) was compared to different farming groups (López-Onaindia & Subirà, 2017), it showed more affinities with Bòbila Madurell (one of the Sepulcres de Fossa groups) than with any other sample.

The aDNA studies that have explored this subject have also observed that the Early- and Middle-Neolithic samples from the North and Northeast of the Iberian Peninsula had diverse genetic signals: some studies showed that Early Farmers presented mitochondrial haplogroups related to those found in Central Europe and Anatolia (Gamba et al., 2012; Haak et al., 2015; Olalde et al., 2015; Sampietro et al., 2007); others (de la Rúa et al., 2015; Hervella et al., 2012), showed that the influence of Hunter-Gatherer genetic background was elevated in the farmer populations from Navarre and the Cantabrian Fringe. A new work including the largest amount of sequenced individuals in the Iberian Peninsula to date shows that the process was heterogeneous in the different areas (Szécsény-Nagy et al., 2017). They observed that during the Early-NeolithicEarly Neolithic the presence of exogenous haplogroups was more common in the Northeast of the Peninsula, while in other areas (such as Upper Ebro Valley and Southwest Iberia) the Hunter-Gatherer profile was more predominant. Moreover, it has also been observed that after this initial mixture of profiles, there was an increase of Hunter-Gatherer ancestry during the Middle-Neolithic and Chalcolithic (Gunther et al., 2015; Haak et al., 2015; Mathieson et al., 2015; Szécsényi-Nagy et al., 2017).

In this sense, comparing our results with samples from outside the Iberian Peninsula (France and Italy) we observe that the Iberian samples from the Mediterranean coast were the most similar to Italian samples, although they considerably diverged from them (López-Onaindia & Subirà, 2017; López-Onaindia et al., 2017). Moreover, this same group was related to coastal Middle-Neolithic samples from Southern France (López-Onaindia et al., submitted b). In contrast, the Solsonian group was more related to French samples from Midi-Pyrenees/Languedoc region (inland) (López-Onaindia et al., submitted b).

These data support an alternative route for the entrance of the Neolithic in the Iberian Peninsula, such as a route from the North throughout the Pyreneans (Zapata et al., 2004).

Besides the common *Impressa-Ligur* and Cardial style pottery found in the Northwest Mediterranean Early-Neolithic, there are also evidences of similarities in culture and active trait between populations from this area during the Middle-Neolithic between Southern France and Northeast Iberian Peninsula. These similarities mainly occurred between the Chasséen culture in France, and Sepulcres de Fossa culture south to the Pyreneans. There were similarities in the funerary culture (Vaquer, 1990) and in many material aspects (Molist et al., 2016). This study suggests that although these two groups were more similar between each other than with any other neighbour culture, each of them had singular elements related to the previous background in the territories. Regarding the exchange networks occurring across the Pyreneans, those seem to be more intense in East-to-West direction than opposite (Gibaja *et al*., 2016 b; Terradas *et al*., 2016). This is observed in the presence of Barrémo-Bédoulian (Honey) Flint from Vaucluse (Provence), polished axes originated in the Alps, and Obsidian blades and nuclei from Sardinia in the structures from the Sepulcres de Fossa group in Catalonia (Binder, 1998; Briois, 2005; Gassin *et al*., 2011; Gibaja *et al*., 2013; Léa, 2004; Léa, 2005; Pétrequin *et al*., 2012; Terradas *et al*., 2014; Vaquer *et al*., 2011). On the other hand, pieces made from Variscite exploited at Can Tintorer mines from Gava (Barcelona) appeared in Chasséen sites to the west of the Rhone (Terradas *et al*., 2016), but this exportation of the minerals occurred after the main exploitation moment of the mines.

Inside the Peninsula there were also exchange networks, for example along the Ebro basin Variscite from Gava's Can Tintorer mines appeared in distant sites such as Paternanbida (Navarre), Cueva de Chaves and Cueva del Moro de Olvena (Huesca) (Baldellou *et al*., 2011). Moreover, although most of the flint used in the Cantabrian area during the Neolithic was from a local origin, between 1 and 10 % of the material was Evaporitic flint from the Ebro's basin (>100 Km), and around 1% came from further areas (>200-300 Km) (Tarriño & Terradas, 2013).

In agreement to the aDNA studies, our results suggested that during the Chalcolithic there is an increase on the proportion of Hunter-Gatherer profile in the human populations, except for the case of the Megaliths from the Cantabrian Fringe. This increase is also observed in the Bronze Age sample that did not show any differences with the Hunter-Gatherers, neither with the Neolithic samples from Navarre. The recent aDNA studies analysing population interactions during the end of the Neolithic have shown that there was continuity between the Chalcolithic populations and Bronze Age ones in the Iberian Peninsula (Olalde et al., 2017; Szécsényi-Nagy et al., 2017), and that there was no population impact related to the Bell-Beaker expansion in the Iberian Peninsula.

In summary, we propose a complex and heterogeneous process of Neolithisation in the Northeast Iberian Peninsula. Moreover, although there are evidences of population influx from Eastern areas of Europe, we have observed that the previous Mesolithic populations had an important impact on the biological composition of later Farming communities, which increased after the first centuries of the Neolithic Age. In addition, we cannot discard any of the two main proposed routes for the arrival of Neolithic communities in the Iberian Peninsula (East from the Mediterranean, and North throughout the Pyreneans), suggesting that both might had happened.

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5. DISCUSION

Depending on the analysed samples, the aDNA studies carried out in Western Europe (Iberian Peninsula and Southern France) show different results regarding the genetic origin of the individuals living during the Neolithic. In this sense, some works suggested that the genetic influence of previous Hunter-Gatherer populations was elevated (de la Rúa *et al.*, 2015; Hervella *et al.*, 2012; Szécsényi-Nagy *et al.*, 2017). Other works (Gamba *et al.*, 2012; Haak *et al.*, 2015; Olalde *et al.*, 2015; Sampietro *et al.*, 2007), on the other hand, showed that the Early farmers of the Iberia Peninsula presented haplogroups similar to those found in Central European groups, originary from the Near-East. Most of these studies are limited in samples, due to the complication of finding appropriate materials in a proper state of conservation that might allow the extraction of DNA. The latest studies have shown that when larger amounts of samples are analysed, the picture broadens and the model that starts to be dilucidated is a combination of both (Szécsényi-Nagy *et al.*, 2017)

This necessity of increasing the sample size in order to understand the process was something obvious when this project was initiated. This should be carried out with a sensitive methodology that would permit the analysis of large samples in an easy, reliable and economic manner. Moreover, it was also interesting that the methodology to be applied would have previously and successfully been used in other European contexts of similar periods.

The study of dental morphology had been proved valuable in studying variations among major human groups, and it had also been applied to the study of the origin of farming in Italy (Coppa *et al.*, 2007) and the dispersion of Corded Ware culture in the end of the Neolithic in Central and Western Europe (Desideri, 2007, 2011).

The benefit of studying teeth in order to determine biological relationships between populations is based on the rapid development of most pieces and the lack of subsequent modification (except for erosion and external pathologies) once they have been formed (Alt & Vach, 1998). Therefore, if any alteration affects the final shape of teeth, this change would be explained genetically or by the effect of environmental disruptions in the short period of development.

In the following segments I will discuss the effects of environmentally produced physiological disruptors in the teeth morphology. Also the characterisation of diverse samples from the different periods and geographical areas, as well as to make a diachronic interpretation of the differences in those profiles.

5.1. THE INTERACTION OF ENVIRONMENTAL DISRUPTORS AND DENTAL DEVELOPMENT AND MORPHOLOGY IN THE SAMPLE

As it has been mentioned before, teeth are overall stable in their development, and most crowns are formed by the age of six. Nevertheless, some studies have shown that this development might be affected by intrinsic (e.g. genetic mistakes and mutations) and extrinsic (environmental disruptors) factors (Bailleu-Forestier *et al.*, 2008 a, 2008 b; Riga *et al.*, 2013).

The outcomes of the disruption have different forms and representations depending on the stage they have occurred at (Brook, 2009). In consequence, some of them strike the observer (e.g. *dens in dente*, macrodontia, *amelogenesis imperfecta*), while others enter into the normal variation (e.g. hypoplasias of the enamel, bigger or smaller expression of concrete traits) that might be expected. When the disruption occurs during the initiation phase, the number or position of teeth is affected; when it occurs during the morphogenesis, size and shape are altered; while when the disruption takes place during the differentiation of the tissues and mineralisation, the dentine or enamel will be affected.

The presence in the sample from Cova del Pantà de Foix of a case of Isolated Bilateral Macrodontia of Lower Second Premolars (López-Onaindia *et al.*, 2014), and other disruption indicators such as high ratios of hypoplasias in teeth (Subirà *et al.*, 2016) and the presence of tumours (multifactorial origin) (López-Onaindia *et al.*, in preparation a) has permitted a broad interpretation of the relationship between environmental factors and dental development.

This case of macrodontia is the first of its kind to be described in archaeological remains. In the previously reported clinical cases no familiar or heritability patterns have been described, as with the exception of one case, the patient did not have any familiar suffering the condition.

The malformation occurred in shape and size, while the specific tissular structures developed correctly. For this reason, the most probable phase of ontogenesis where the disruption happened is during morphogenesis. One of the key factors regulating morphogenesis is apoptosis, and it has been described that a disruption on this type of cell death might lead to macrodontic phenotype (Kassai *et al.*, 2005; Kim *et al.*, 2006). The control of development induced by apoptosis is especially important in the end of activity of the Enamel Knots (EK) (Matalova *et al.*, 2012). These structures are responsible of segregating those growth and transcription factors that induce the proliferation of mesenchymal and surrounding epithelial cells, and produce the folding of the epithelium leading to the cusp pattern of the teeth. Bone Morphogenetic Proteins (BMPs), *p21* and *Ectodine* seem to be crucial in silencing embryonic signalling centres (Jernvall *et al.*, 1998; Kassai *et al.*, 2005). An inheritable mutation on any of these genes might lead to generalised forms of macrodontia, which has been related to different syndromes (e.g. gigantism, insulin-resistant diabetes, KBG syndrome, otodental syndrome, or facial hemihyperplasia) (Dugmore 2001, Fuentes & Borie 2011, Canoglu *et al.*, 2012).

As the case is isolated in antimeric teeth (similar developmental timing), it is likely that the anomaly on the regulation of apoptosis was punctual. An origin is probable taking into account the other indicators of physiological disruption due to environmental factors (high ratios of hypoplasias and presence of tumours), and the evidences that point out that BMPs might be down regulated due to epigenetic processes related to environmental stressors (Riga *et al.*, 2013).

Bilateral asymmetry of the structures can be divided in three main groups: 1) directional asymmetry, 2) antisymmetry, and 3) fluctuating asymmetry. Directional asymmetry is the one that occurs when one of the antimere is consistently more developed than the other in a population (Graham *et al.*, 1993; Markow, 1995; Palmer, 1996). Antisymmetry is defined when asymmetry is present in the majority of a population, but without a dominant side (Graham *et al.*, 1993; Markow, 1995; Palmer, 1996). Fluctuating asymmetry (FA) occurs when one side is not favoured relative to the other in a population, and the deviations are slight (Klingenberg & Nijhout, 1999; Palmer & Strobeck, 1986; Palmer, 1996). Many studies suggest that environmental disruptors of development cause FA (e.g. malnutrition, extreme temperatures and parasites) (Markow, 1994, 1995; Woolf & Markow, 2003).

FA is considered in dental morphology in two cases: when a given trait can be found on one antimere but not in the opposite; or when it is expressed in a different grade in each side (Bollini *et al.*, 2009; Rizk *et al.*, 2008; Scott & Turner, 1997).

As it has been reported, the expressions of genes taking part during ontogeny can be highly affected by environmental factors, and it happens in dental development as well (DeLeon, 2007; Riga *et al.*, 2013; Rizk *et al.*, 2008; Salazar-Ciudad & Jernval, 2002, 2010; Scott & Turner, 1997). In fact, developmental precision (the concept opposed to developmental instability) is based on the ability of the organism to respond to genomic guidance during ontogeny. This process is determined by two opposing factors: 1) Developmental Instability, which hampers the ability of keeping precision; and 2) Developmental Homeostasis, based on the organisms' ability to redirect towards bilateral symmetry after perturbation. This ability to maintain homeostasis might have genetically determined limitations (Palmer, 1996). Therefore, FA occurs as a result of the interplay between environmental disruptors and genetic responses (Klingenberg & Nijhout, 1999). For this reason, FA can be used to measure developmental instability.

In the case of dental morphology, few studies have analysed the relationship between Fluctuating Asymmetry and developmental instability, as in the last 35 years only 4 papers have been published on the subject (Bollini *et al.*, 2009; Marado *et al.*, 2017; Mayhall & Saunders, 1986; Noss *et al.*, 1983).

Our results, presented at the 2017 StressedOut Conference in London (Appendix I) suggest that asymmetry in dental non-metric traits was a common feature in different analysed samples (Cova del Pantà de Foix, Bòbila Madurell, and Camí de Can Grau), as the prevalence of asymmetric traits when we combine the samples is 80%. Most of these asymmetric traits occur in a random mode, and therefore can be identified as FA. Nevertheless, and although the amount of analysable traits in the sample is scarce, Cova del Pantà de Foix did not present the most elevated ratios of asymmetric traits.

Marado and collaborators (2017) successfully detected differences in FA ratios between sexes in 19th and 20th century samples from Portugal. These differences have their explanation in registered social patterns where conditions for girls would be worse than for boys. Therefore, this study validates the use of dental fluctuating asymmetry as a measure of developmental instability.

Although we were not able to find the expected differences between samples, we found some logic patterns in the results. First, we observed that those teeth that were asymmetric in a larger amount of individuals are the ones that form last. Moreover, these teeth undergo morphogenesis at the same moment as I2s and Cs get mineralised, which are the two types of tooth presenting the higher ratios hypoplasias.

It might be assumed that asymmetry in these traits is usual. In fact, on the standardised protocol for recording dental morphological traits and using them to calculate biological distances it is assumed that both antimeres might score different, and there is a protocol to select the one showing the highest level of expression (Scott &Turner, 1997; Turner *et al.*, 1991).

The aftermat of these results, although we must be careful due to the small analysed sample size, is that we can sense that from this baseline on dental ontogenesis is pretty conservative. In this sense, we observe that a presumably more disrupted sample does not present higher ratios of asymmetry. This might also be related to the disruption happening in Cova del Panta de Foix at a moment when it would not affect morphogenesis, but we have observed with the case of Isolated Bilateral Macrodontia of Lower Fourth premolars that this is not the case, as well as the first and second incisors, and canines presented high ratios of hypoplasias too.

In summary, we propose that dental morphology is stable enough at a population level to be a useful tool to study biological affinities between human groups, even in highly disruptive environments. This was suggested by Scott and Turner (1997), as they observed that, although some individuals might be more affected by environmental factors, the effect of those in tooth morphology at the population level would not be significant.

5.2. CHARACTERISING THE MESOLITHIC AND NEOLITHIC GROUPS FROM THE IBERIAN PENINSULA BY MEANS OF DENTAL MORPHOLOGY

Some concrete populations from Western Europe have shown that they retain differences on their genetic diversity compared to other groups from the area. These groups are mainly the Basque (in the North of the Iberian Peninsula and Southern France), and the Sardinian (Bauduer, 2017; Behar *et al.*, 2012; Cardoso *et al.*, 2011; 2013; Cavalli-Sforza *et al.*, 1994; Gunther *et al.*, 2015; Rodríguez-Ezpeleta *et al.*, 2010 Wilson *et al.*, 2001). In many times, the differences these groups present have been related to isolation processes that date back to the expansion of the Neolithic (Behar *et al.*, 2012; Cardoso *et al*, 2011, 2013; Günther *et al.*, 2015).

In a work from 2013, Scott and collaborators define the Eurodont dental pattern to distinguish Western European morphology from that of other European areas (Caucasoid dental complex) and the world. They determined that the main characteristics of the Eurodonts are the following:

- Low frequency traits: UI1 winging (<0.09), UI1 shovelling (<0.083), UI1 double shovelling (<0.03), Bushman Canine (<0.022), UM1 enamel extension (<0.032), LM2 Y groove pattern (<0.235), LM1 cusp6 (<0.182), LM1 cusp7 (<0.088), LM1 protostylid (<0.023), LM1 deflecting wrinkle (<0.435), and 3 rooted LM1 (<0.013).

- High frequency traits: UM1 Carabelli (>0.567), LP4 lingual cusps (>0.514), UM2 absence of hypocone (>0.184), LM1 4 cusps (>0.076), LM2 4 cusps (>0.850), and LC 2 roots (>0.097).

When we compare the frequencies obtained for most of our samples with that of the Eurodont dental pattern we observe that they overall fit into it (Hunter-Gatherers and Neolithic and Post-Neolithic). The sole trait that differs in all the prehistoric samples compared to that of historic and current samples is the presence of Carabelli’s trait, which is lower in the former.

5.2.1. Testing the biological homogeneity of the different Neolithic groups from the northeast of the Iberian Peninsula: focusing on the chronology, geographical dispersion of the groups and the cultural variability during the period

Although all the studied farmer samples from the Iberian Peninsula (López-Onaindia & Subirà, 2017; López-Onaindia *et al.*, 2017; López-Onaindia *et al.*, submitted a,b; López-Onaindia *et al.*, *in preparation*; Subirà et al., 2016) share presence frequencies for the traits within the margins of the Eurodont dental complex (Scott *et al.*, 2013), there are some significant biological differences between some of the groups. These differences were more visible during the Middle-Neolithic than in the Late-Neolithic, and disappeared or got reduced at the end of the Chalcolithic and Bronze Age.

We have analysed two main groups belonging to the Middle-Neolithic in the Northeast of the Iberian Peninsula that diverge in the funerary traditions: the pit burial-related *Sepulcres de Fossa* group, which as in the Late phase of the Early Neolithic inhumated the individuals in pits excavated in the soil (Gibaja, 2004); and the Solsonian group, characterised by the cists, semi-megalithic tombs created with stone-slabs (Castany, 2009). These two types of burials are also found North to the Pyreneans.

In the Iberian Peninsula the cists are found in mountainous areas from the Catalan Pre-Pyreneans and in the Pyreneans, while the pit graves appear near the Mediterranean, and some Early Neolithic samples in the Ebro basin in Navarre. The grave-goods found in both type of sepulchres indicate extensive exchange networks within the Iberian Peninsula and with other Mediterranean areas (Vauclusean Honey flint, or Obsidiane from Sardinia are found overall). Moreover, the stable isotope analyses found not dietary differences between the two groups (Fontanals-Coll *et al.*, 2017). In contrast, the two groups are significantly different in biological terms based on their dental morphology (López-Onaindia *et al.*, 2017; López-Onaindia *et al.*, submitted a). Nevertheless, none of the two groups significantly diverges from the Early- and Middle-Neolithic samples from Navarre (López-Onaindia *et al.*, submitted a). These differences are mainly explained due to higher frequencies of 4 cusped LM2 and presence of cusp 5 in LM3 in the Pre-Pyrenean sample compared to the others. In contrast, a study analysing the differences between individuals found in pits from different coastal regions showed that there were no significant differences between them (Pascual *et al.*, 2016).

The aDNA studies performed to date have shown that Early-Neolithic samples from North-eastern Iberian Peninsula resembles to that found in Early-Neolithic from Anatolia, Carpatian Basin, and Central Europe (Haak *et al.*, 2015; Olalde *et al.*, 2015). Moreover, the Early- and Middle-Neolithic Pyrenean sample of Els Trocs lacks the typical Iberian Hunter-Gatherer haplogroups. The samples that kept Hunter-Gatherer lineages in their genetic make-up in greater scale where those Early-Neolithic groups from Navarre. Moreover, it has been suggested that these groups were genetically diverse (Hervella *et al.*, 2016). During the Middle-Neolithic and Late-Neolithic the Hunter-Gatherer genomic signal was again more common in more Eastern territories (Szécsényi-Nagy *et al.*, 2017). At this period (Middle-Neolithic), there is also a genetic link between samples from Northeast Iberia and Southeast France (Szécsényi-Nagy *et al.*, 2017), two areas that show mutual technological and typological influences, as well as evidences of trade networks (Gassin *et al.*, 2006, 2011; Gibaja *et al.*, 2013; Léa, 2004, 2005; Pétrequin *et al.*, 2012; Vaquer *et al.*, 2011).

In fact, we compared Middle-Neolithic samples from these two related areas (Southern France and Northwestern Iberian Peninsula) analysing the Dental morphology, and the results show that these groups are similar in many aspects, although there are some comparisons that scored significantly different (López-Onaindia *et al.*, submitted a). In these analyses, we observed that the Montbolò sample from the Pyrenean area shared high affinities with all the Middle-Neolithic samples from both sides of the Pyreneans, and only showed some slight differences with the Early-Neolithic sample of Los Cascajos from Navarre.

On the other hand, although none of them showed differences with this previous group, differences were observed between the Midle-Neolithic samples. As it has previously been mentioned, the Solsonian and more coastal groups diverged in the Iberian Peninsula. Another group that showed significant differences with these coastal sites, but also with the Navarran group is the Midi-Pyrenees/Languedoc sample. This sample is composed by sites that are found both near the coast and in the inland (near Toulouse), and it is the one also presenting some burials in cists (Loison *et al.*, 2004; Loison & Schmitt, 2009). In fact, the Iberian group to which it was less different is the Solsonian one. In the case of the Provençal samples, these did not show any significant differences neither with the other French sample nor with the Iberian ones. The Provence is the area where the Vaucluse Honey flint found in Northeastern sites from the Iberian Peninsula is produced and a suggested distribution zone for the Sardinian obsidian along the continental lands (Gibaja *et al.*, 2013; Terradas *et al.*, 2014, 2016). Therefore, it seems plausible that due to the intense exchange networks this sample had more biological affinities with the rest of the analysed samples.

These differences got reduced during the Chalcolithic and in the Bronze Age, when most funerary practices consisted on collective burials. The only exception to this tendency occurs in the Solsonian area and with the Megalithic monuments from the Basque country, which presented differences with other Chalcolithic samples (López-Onaindia & Subirà, 2017; López-Onaindia *et al.*, 2017). In these two cases the analysed samples are small, and all interpretations should be cautious. What it seems to follow a pattern it is that there was not a major population substitution in the transition from Middle-Neolithic to the Chalcolithic in each area.

This continuity is also identified in the aDNA (Szécsényi-Nagy *et al.*, 2017). In this work the researchers identified that the genetic composition of Chalcolithic samples was similar to the Midle-Neolithic farmers in each region, with a high presence of Hunter-Gatherer lineages. This continuity would go on in the Bronze Age, as few signals of "steppe ancestry" are found in Iberian samples related to Bell-Beakers (Olalde *et al.*, 2017; Szécsényi-Nagy *et al.*, 2017). In fact, some of the previous wide exchange networks seem to have disappeared during the chalcolithic and new ones created regarding the evidences in raw materials. Furthermore, studies that have been realised in order to understand the dichotomy on burial expressions in the North of the Peninsula during the Chalcolithic (caves and megaliths), (Fernández-Crespo & de la Rúa, 2016).

On the other hand, recent analyses in dental morphology from Chalcolithic samples from the South of the Peninsula, suggest the presence of traits that can be related to a North-African ancestry. these evidences might be related tothat of raw materials from this continent, including Ivory, found in Southern areas of the Iberian Peninsula (Irish *et al., 2017*).

5.2.2. Testing the biological homogeneity of the Mesolithic samples from different areas of the Iberian Peninsula

The results indicate that all the Mesolithic samples from the Iberian Peninsula shared the same biological origin, as there were no significant differences between the Hunter-Gatherers from Portugal and Mediterranean areas or North of the Peninsula (López-Onaindia *et al.,* submitted b). Moreover, the morphological data indicate that these Iberian samples differ from their coetaneous samples from Italy. The samples that have been analysed for this dissertation share many of the Eurodont features, although in many of the traits the frequencies are more extreme (lower ratios of UM1cusp 5, of UI2 tuberculum dentale, and LM1 cusp 6) than those proposed by the authors describing the morphotype (Scott *et al.*, 2013). The only trait that does not concord with the

Eorodont dentition was the low ratios of UM1 Carabelli in the Iberian sample. In the case of the Italian sample (Coppa *et al.*, 2007), we have compared the ratios for the traits to those of the Eurodont morphotype and overall, it shares many characteristics. Nevertheless, we observe that the Italian Hunter-Gatherer sample is different from the Eurodonts in the fact that they present low frequencies for multiple cusped LP4, 4 cusped LM2, high frequencies of interruption grooves in UI2, and all the individuals presented 5 cusped LM1.

Previous analyses in aDNA have shown that, effectively, Hunter-Gatherers from the Iberian Peninsula differ from those from other areas of Europe, Italy included (Hervella *et al.*, 2012; de la Rúa *et al.*, 2015). Moreover, the analysed Iberian samples present certain homogeneity among them presenting high frequencies of haplogroups H (43.8%) and U5b (37.5%), and low for those more general in Central European samples from the same period U2 and U5a (Hervella *et al.*, 2012; de la Rua *et al.*, 2015; Sánchez-Quinto *et al.*, 2012; Szécsényi-Nagy *et al.*, 2017). In the case of haplotype analysis though, the Iberian Hunter-Gatherers had higher diversity than the Central European Hunter-Gatherers (Szécsényi-Nagy *et al.*, 2017).

The Iberian Peninsula was one of the few European inhabitable areas during the Last Glacial Maximum, because together with Italy and the Southeastern part of Europe it was warmer than other areas of the Continent (Bañuls-Cardona *et al.*, 2014; Soomer & Nadachowski, 2006). This made the Peninsula one of the areas with most extensive archaeological register during this period (Gamble *et al.*, 2005; Garate *et al.*, 2014, 2015). Once the Last Ice Age finished and the Holocene started the remaining parts of Europe populated from these refuges (Achili *et al.*, 2004; Gamble *et al.*, 2005; Pereira *et al.*, 2005; Soares *et al.*, 2010; Torroni *et al.*, 2001). For this reason, and although population influx into the refuges could be possible, it is more plausible that the main demographic tendency was exit from the same. Therefore, the admixture between individuals evolving for centuries in each of the refuges would happen in the new inhabitable areas and not inside the refuges themselves.

5.3. ANALYSING THE BIOLOGICAL AFFINITIES BETWEEN MESOLITHIC AND NEOLITHIC GROUPS OF THE NORTHEAST OF THE IBERIAN PENINSULA AND SURROUNDING AREAS

When the Hunter-Gatherer samples and Farmer samples were compared (López-Onaindia *et al.*, submitted b; López-Onaindia *et al.*, in preparation b), we observed that there was not a clear separation from the formers' background in the second group. In both works the tendency was that the Middle Neolithic sample from near the Mediterranean coast was more divergent from the Mesolithic than the Early Neolithic samples from Navarre (Upper Ebro Valley). Nevertheless, these distances were not as large as those any of the groups had with the Italian samples, for example. Furthermore, the late Neolithic samples were more similar compared to the Pre-Neolithic ones than the Middle Neolithic samples. As mentioned before, in the case of the samples from this latter period, we have been able to distinguish two biologically different groups in the Northeast of the Peninsula related to different funerary practices: The Solsonian group and the *Sepulcres de Fossa* group.

Related to the Hunter-Gatherer samples, the Solsonian group presented slightler differences with them than the Sepulcres de Fossa group. Moreover, this group from the Pre-Pyreneans and Pyreneans also presented some affinity degree to samples to the North of the Pyreneans (Midi-Pyrénées/Languedoc region), while the most coastal groups were more related to coastal groups from Southern France (Provence). In addition, when the samples had been compared to Italian ones, the Mediterranean coastal groups happened to be less different from them than the inland mountain ones.

The oldest archaeological evidences for the presence of the Neolithic in the Northeast of the Iberian Peninsula appear in the Mediterranean area (Guixeres de Vilobí, El Barranquet, La Draga, Can Sadurní, and Cova Bonica) and in the Pyreneans (Els Trocs, Chaves, and Balma Margineda) (Bernabéu *et al.*, 2011; Oms *et al.*, 2014, 2016; Rojo *et al.*, 2015). In fact, the individuals from the Early-Neolithic site of Els Trocs (Huesca) showed genetic profiles that linkt them with Anatolia and Central Europe (Haak *et al.*, 2015). Moreover, an individual from the Cardial period recovered in Cova Bonica also showed genetic similarities with Neolithic individuals from central Europe (Olalde *et al.*, 2015). On the other hand, Early Neolithic individuals from the Upper Ebro valley presented high diversity of haplogroups, which were both new haplogroups in the Peninsula and previously present ones in the Mesolithic communities (de la Rúa *et al.*, 2015; Hervella *et al.*, 2012, 2016). These data show that at least the impact of incoming populations in the Iberian Peninsula at the beginning of the Neolithic period was different in the various areas of the Peninsula. Moreover, although the most accepted route for the influx is the Mediterranean coastal one, the results show that somehow immigration occurred from the north of the Pyrenees. This alternative route has also been proposed based on archaeobotanical evidence (Zapata *et al.*, 2004). Our results do not discard any of them, and suggest that both might happen: an influx from the Mediterranean influencing the biological pattern of more coastal areas, while the immigration from the North of the Pyrenees would have influenced the profile of groups from the mountain areas.

In our case, except for the samples from the Upper Ebro Valley, we do not have enough samples in the Northeast of the Peninsula to analyse the differences between the Early Neolithic communities and the Middle Neolithic communities. Nevertheless, aDNA analyses have shown that the Hunter-Gatherer elements increased in the samples posterior to the farming bloom occurred in this transition (Gunther *et al.*, 2015; Haak *et al.*, 2015; Mathieson *et al.*, 2015; Szécsényi-Nagy *et al.*, 2017). Szécsényi-Nagy and collaborators (2017) observed that the increase on hunter-gatherer ancestry was a trend that continued after the middle Neolithic and into the Chalcolithic, suggesting a continuity on the populations of these periods. Our results have shown this trend as well, as Chalcolithic samples show fewer differences with the Hunter-Gatherer sample. Furthermore, the Bronze Age Iberian samples show no differences with the Pre-Neolithic one. Related to this, the recent aDNA studies have shown that there was continuity between the Chalcolithic populations and Bronze Age ones (Olalde *et al.*, 2017; Szécsényi-Nagy *et al.*, 2017), and that there was no population impact related to the Bell-Beaker expansion in the Iberian Peninsula.

6. CONCLUSIONS

1. Dental morphology is a reliable tool to address the analysis of population affinities in the transition from the Mesolithic to the Neolithic in the Iberian Peninsula, and the biological relationships inside each of the periods. This is proved as the present results resemble those obtained via aDNA.

2. Although dental morphology might environmentaly be affected in indivual and populational level, the later is rather difficult and the ontogenetic process is stable.

3. The biological origin of Neolithic populations from the Iberian Peninsula was heterogeneous, and differences are observed in relation to geographical areas and funerary cultures.

4. The Mesolithic samples from the different areas of the Iberian Peninsula shared the same biological origin, which might be related to the isolation of the populations in the Peninsula during the Last Glacial Maximum.

5. The Neolithic populations from the Northeast of the Iberian Peninsula preserved biological signals of the Hunter-Gatherers, which increased after the Middle-Neolithic. The Neolithic samples that presented a more elevated degree of affinity to the Mesolithic ones were those from the Cantabrian Fringe and Upper Ebro Valley

6. During the Early-Neolithic populations entered in the Peninsula from two possible ways, the Mediterranean Coast and from the Pyrenees.

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8. APPENDIX

Appendix I

Results presented at the StressedOut conference in UCL (London) may 19th, 2017

The results on the analysis for the presence of hypoplasias on teeth showed, as observed in Subirà and collaborators (2016), that the presence of dental hypoplasias in Cova del Pantà de Foix was elevated. In fact, 35.7 % of teeth in Cova del Pantà de Foix presented at least one Linear Enamel Hypoplasia (LEH), a prevalence that is more than double of that observed in Cami de Can Grau (13.6 %) and Bòbila Madurell (9.9 %) (Table I.1). When data were analysed by individuals, Cova del Pantà de Foix still presented the most elevated ratios of individuals presenting at least one tooth with LEH, but the differences were not so large among the different analysed collections (Table I.1).

In Figure I.1, the presence of hypoplasias is shown per type of tooth and for each of the analysed samples. With this organisation of the data it is also observable that Cova del Pantà de Foix had higher prevalences of LEH for every type of tooth than the other two samples. Nevertheless, we observed that the differences were smaller when it came to Canines and Upper lateral incisors.

In the case of the analysis of the asymmetry, when the three samples were combined, 72 variables presented a sample size big enough for interpreting the results (Table I.2). From these variables 84% were asymmetric in at least one individual, and 60% of these asymmetric traits could statistically be determined as Fluctuating Asymmetric (FA).

When the data were separated by samples (Table I.2), the number of traits that were bilaterally recorded in acceptable numbers decreased. Nevertheless, we observed that those samples were more variables were analysed presented higher ratios of asymmetric ones, while in Cova del Panta de Foix few variables (9) could properly be analysed, those mainly corresponding to first molars. For this reason, this sample presented the lowest ratio (66.6 %) of asymmetric traits from the analysed ones. However, 83% of these asymmetric traits were due to Fluctuating asymmetry.

In figure I.2 we show the ratios of asymmetric individuals for the traits that were comparable between the three samples. We observed that, in most of the cases, Bòbila Madurell was the sample where more individuals were asymmetric for each of these traits, while in Cova del Pantà de Foix the ratios were either the lowest or intermediate.

Finally, the trait that was scored as asymmetric in more individuals among the three samples was the *lingual cusp number of LP4*, as 68.1 % of the individuals were asymmetric for it. These teeth and the others that presented higher ratios of asymmetry (UM2, UM3, LM2 and LM3), which undergo morphogenesis when second incisives and canines are getting mineralised.

Table I.1. Summary of the presence of hypoplasias by teeth (first two columns) and by individuals (last two columns) in the three analysed samples. In the case of the analysis by individuals in cova del Pantà de Foix it as been divided by upper jaws and mandibles.

	Analysable teeth	**% of present hypoplasias (LEH)**	**Analysable Individuals**	**% of individuals with hypoplasias (LEH)**
Cova del Pantà de Foix	288	35.76	15	73.33
			20	60.00
Camí de Can Grau	190	13.68	20	45.00
Bòbila Madurell	541	9.98	55	54.55

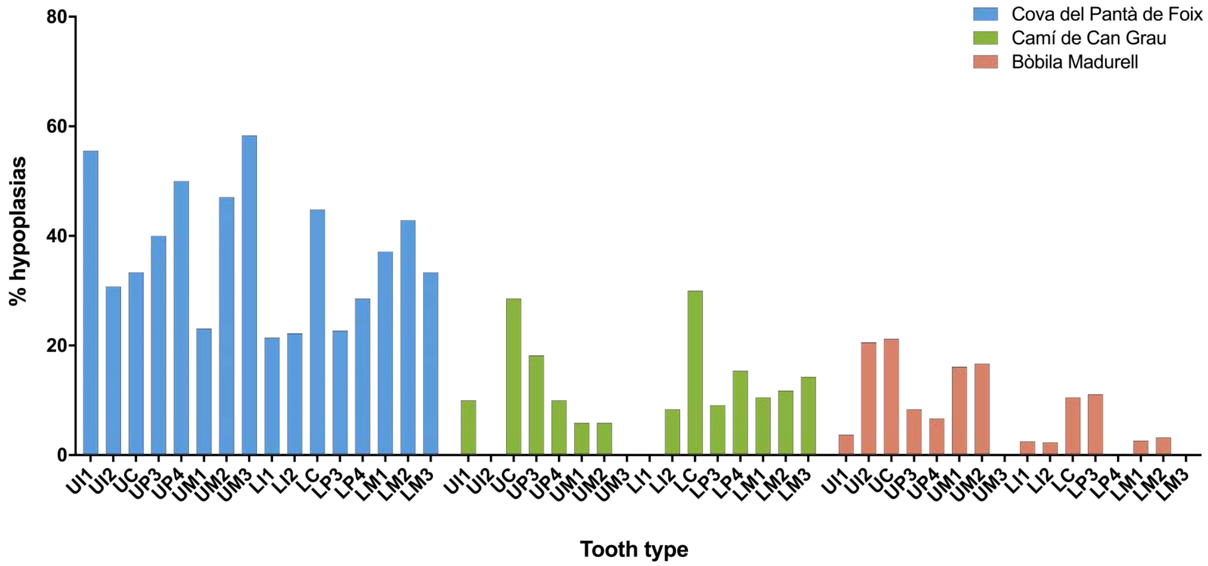

Figure I.1. Percentages of presence of hypoplasias by each type of tooth in the three studied samples.

Table I.2. Data regarding the asymmetry in all the combined samples (first row) and each of them separately.

	N traits	% asyric traits	% of FA traits	% of FA traits among asymmetric traits
All groups	72	84.722	51.388	60.655
Cova del Pantà de Foix	9	66.666	55.555	83.333
Camí de Can Grau	35	71.428	45.714	64
Bòbila Madurell	56	80.357	53.571	66.666

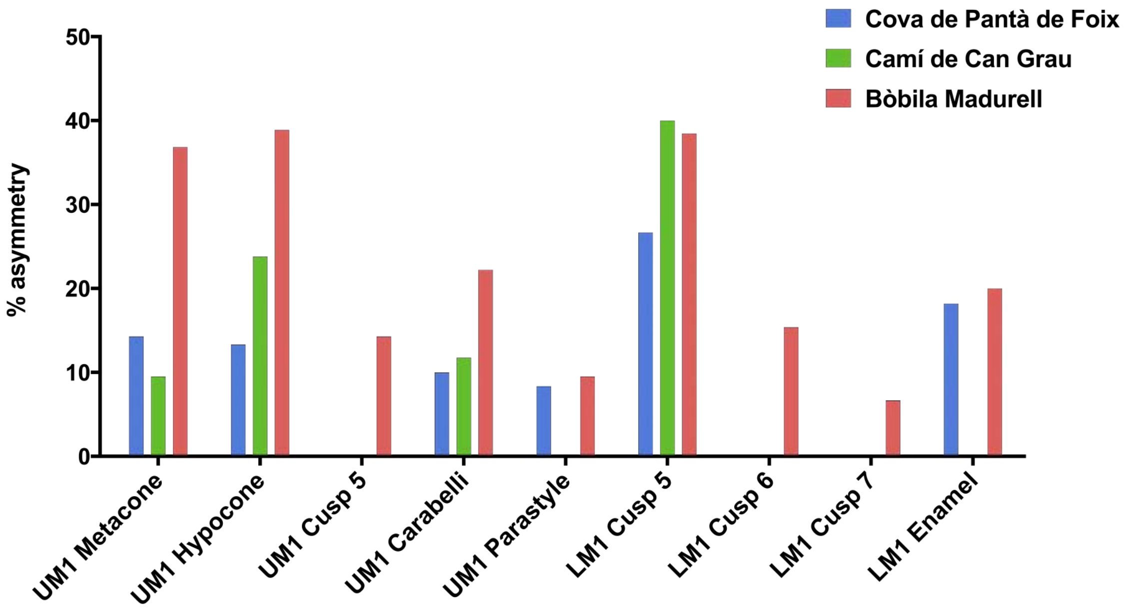

Figure I.2. Comparison of the percentages of asymmetric individuals in each sample for the 9 comparable traits among them.